The Dissertation Committee for Sarah Elizabeth Allen Certifies that this is the approved version of the following dissertation:

Procedural Memory Consolidation in Musicians

Committee:

Robert A. Duke, Supervisor

Lowell J. Bethel

Eugenia Costa-Giomi

Jacqueline C. Henninger

Judith A. Jellison

Laurie P. Scott

Procedural Memory Consolidation in Musicians

by

Sarah Elizabeth Allen, B.M., M.M.

Dissertation

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

Doctor of Philosophy

The University of Texas at Austin

August 2007

Dedication

I would like to dedicate this dissertation to my husband, B.J. Allen,

and to my parents, Carolyn and Joe Callan.

Procedural Memory Consolidation in Musicians

Publication No._____

Sarah Elizabeth Allen, Ph.D.

The University of Texas at Austin, 2007

Supervisor: Robert A. Duke

Procedural memory consolidation has been shown to enhance a variety of perceptual and motor skills during sleep. Only recently has this effect been investigated in trained musicians performing music. I tested the extent to which a music performance skill benefited from sleep-based consolidation overnight and whether this process may be inhibited when musicians learn two melodies in juxtaposition.

60 experienced musicians, all nonpianists, learned to perform either one or two 13-note piano melodies during evening training sessions. The musicians practiced each melody with their nondominant hand by repeating it from beginning to end during 12 30-second practice blocks alternating with 30-second rest intervals. All participants were retested on the target melody the following morning in three 30-second retest blocks alternating with 30-second rest intervals.

Participants who learned only one melody in the evening showed overnight gains in the number of correct key presses per block (CKP/B) in the target melody at retest. Participants who learned the target melody and an additional melody at training showed no overnight gains in CKP/B in the target melody. Participants who learned both melodies and then immediately were retested on the target melody at training showed overnight gains in CKP/B in the morning retest of the target melody—gains similar to those observed among the participants who learned only the target melody at training; this group showed no decrement in the performance of the target melody in the retest at the end of training, which indicates that there were no immediate interference effects apparent in the target melody after having learned the second melody.

These results show that experienced learners performing a familiar type of task, and one that includes auditory processing demands, benefit from overnight consolidation of procedural memories. These benefits may be inhibited, however, when musicians learn similar, competing tasks in juxtaposition.

Table of Contents

List of Figures

I. INTRODUCTION

Accomplished musicians have spent thousands of hours in concentrated practice, learning and refining the fundamental technical skills necessary to play or sing with seeming effortlessness. Achieving such a high level of technical command allows them to convincingly convey ideas, moods, and emotions to listeners through music.

Although the content of practice sessions and the strategies employed to develop and maintain skills have been the topics of some research in music, much remains to be understood about the cognitive and physical mechanisms that lead to the mastery of intricately complex skills like music performance. Repetition is certainly a central element in the development of observable improvement over time, but the neural mechanisms underlying these behavioral improvements are just beginning to be elucidated. Of course, it is possible to learn, practice, teach, and perform music well without a great deal of insight into these underlying processes, as musicians have been doing for hundreds of years, but a deeper understanding of the fundamental machinery of motor learning will not only clarify the nature of developing skills, but may also suggest strategies for maximizing the effectiveness of practice and pedagogy.

Over the past century, researchers have addressed the topic of music practice in relation to performance and pedagogy. Much of the current understanding of music practice comes from studies on music memorization (Chaffin, Imreh, & Crawford, 2002; Rubin-Rabson, 1939, 1940, 1941a, 1941b, 1941c), "deliberate" practice (Ericsson & Charness, 1994; Ericsson, Krampe, & Tesch-Romer, 1993; Madsen, 2004; Maynard, 1999; Sloboda, Davidson, Howe, & Moore, 1996), modeling (Goins, 2006; Hewitt, 2001; Rosenthal, 1984), mental practice (Coffman, 1990; Rosenthal, Wilson, Evans, &

Greenwalt, 1988; Ross, 1985), and organization of practice (e.g., Duke, Davis, & Simmons, 2004; Maynard, 1999; McPherson, 2005; Williamon, 2002; Williamon & Valentine, 2000). This line of research has revealed much about the practice behaviors of expert musicians and the variety of effective strategies musicians use to effect change in their own performance.

In addition to this growing body of research in music, recent studies of neuroscience, aided by significant advances in imaging technology, have begun to reveal physical characteristics of musicians' brains that form the foundation for their physical and auditory skills (e.g., Classen, Liepert, Wise, Hallett, & Cohen, 1998; Pantev, Engelien, Candia, & Elbert, 2001; Parsons, 2001; Schlaug, 2001). Still, despite the many aspects about musicians' perceptual, cognitive, and motor skills that are illuminated in these studies, there is still a need in music research to understand more fully the processes underlying skill learning and refinement.

A substantive body of relevant research into the nature of skill learning has emerged outside of music, predominantly in the fields of kinesiology, psychology, and neuroscience. For example, studies in kinesiology have explored many of the behavioral aspects of motor skill learning: the effects of learner's knowledge of results during practice (Lai & Shea, 1998; Swinnen, Schmidt, Nicholson, & Shapiro, 1990; Wulf, Lee, & Schmidt, 1994); contextual interference (Shea, C. H., Kohl, & Indermill, 1990; Shea, J. B. & Graf, 1994; Young, Cohen, & Husak, 1993); practice variability (Giuffrida, Shea, & Fairbrother, 2002; Kerr & Booth, 1978); and learners' focus of attention (McNevin, Shea, & Wulf, 2003; Shea, C. H. & Wulf, 1999; Wulf, Mc Connel, Gartner, & Schwarz, 2002). Studies in neuroscience and psychology have revealed much about the neural substrates underlying the learning and refinement of skills; research on learning and memory has received much attention over the past half-century and the field has made particularly

large advancements in the past 15 years (for reviews, see McGaugh, 2000; Walker & Stickgold, 2006). Of particular interest to musicians and other skilled learners, the topics of skill learning and the formation of procedural memories have more recently received considerable attention; however, the field of music is only beginning to integrate the findings of this recent research into our understanding music performance.

How procedural memories are encoded, how they are integrated into a learner's memory store, and how they are later retrieved and then reintegrated into existing memory are processes that remain obscure. The timeline of neural changes associated with practice is also not entirely clear, nor are the factors that can interfere with memory storage and retrieval, the conditions that best facilitate learning and transfer, and the changes in synaptic organization that make a memory more or less "permanent."

What is clear is that during practice on a new procedural skill, such as playing an instrument, the brain begins to construct and store an internal representation of the skill. Continuing practice over time typically yields observable improvements in performance, with the behavioral gains obtained during active practice traditionally regarded as the measure of learning. Task repetitions serve to further strengthen and refine this representation.

Research on this topic more recently has revealed that additional learning (i.e., the refinement and enhancement of skills) can occur after active practice has ended. Although behavioral improvements in performance parameters like speed and accuracy are usually observable within a given practice session, further learning may continue long after practice has ended, as evidenced by continued activation and changes in the brain and additional gains in performance over time. It is now understood that changes in the brain during the minutes and hours following initial practice of novel skills serve to stabilize procedural memories, rendering them less vulnerable to interference by other,

competing stimuli (Walker, Brakefield, Hobson, & Stickgold, 2003). This stabilization process begins during active practice and continues throughout the subsequent hours, independent of further rehearsal or awareness, with the new memories demonstrating increased stability and resistance to interference 6 hours after practice has ended (e.g., Brashers-Krug, Shadmehr, & Bizzi, 1996; Walker, Brakefield, Hobson, & Stickgold, 2003). This process of neurophysical modification of synaptic structures, termed *memory consolidation*, comprises two parts: consolidation-based stabilization, which occurs during waking hours following practice, and consolidation-based enhancement, which typically occurs during sleep (Walker, 2005).

During the period of sleep following practice, further changes and refinements continue in the brain, reflected in performance gains evident the next day (Brashers-Krug, Shadmehr, & Bizzi, 1996; Cohen, Pascual-Leone, Press, & Robertson, 2005; Duke & Davis, 2006; Korman, Raz, Flash, & Karni, 2003; Simmons & Duke, 2006; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002). Post-sleep performance typically exhibits performance improvements in accuracy and speed, behavioral manifestations of the underlying molecular consolidation process.

Neuroimaging techniques have revealed that the portions of the brain associated with skill learning remains quite active over the period of wake in the hours following practice (Peigneux et al., 2006). During this time, several "offline" processes take place, including gene expression and the synthesis of new proteins, the creation of new synaptic connections, the "unmasking" of existing synaptic connections, and a reduction in the amount of energy needed to trigger particular synaptic circuits, a process known as *long-term potentiation.*

The timeline of offline events following skill practice is not exactly known, and several methods have helped researchers examine these offline processes more closely.

The creation of new proteins is essential to neural plasticity following learning, and this process of protein synthesis has been studied by injecting chemical protein synthesis inhibitors (known to stop the growth of new synaptic terminals) into the brain. For example, by injecting anisomycin into a rat's brain following the learning of a shock-avoidance task, the new memory can be erased entirely (Milekic & Alberini, 2002; Trepel & Racine, 1999). Injecting the same solution hours later, after the new memory has had time to stabilize, results in no performance decrement. This research provides evidence that new memories are fragile during the period following practice, in part because of the time required to reorganize the synaptic connections involved in memory storage.

Other techniques have illuminated post-training neural processes as well. Repetitive transcranial magnetic stimulation (rTMS), a non-invasive procedure that sends a focused magnetic field to a specified location in the brain, is known to suppress activity in a targeted brain region in humans (Baraduc, Lang, Rothwell, & Wolpert, 2004; Muellbacher et al., 2002). It has been demonstrated that rTMS applied over the primary motor cortex immediately following practice on a simple motor task disrupts practice-related gains, typically returning performance to baseline levels. However, rTMS introduced 6 hours following practice has no negative effect on learners' subsequent performance.

It has also been demonstrated that learning two novel tasks in succession may reduce or eliminate the consolidation-based gains that would typically be observed in the performance of the first task following sleep (Brashers-Krug, Shadmehr, & Bizzi, 1996; Dorfberger, Adi-Japha, & Karni, 2007; Fischer, Nitschke, Melchert, Erdmann, & Born, 2005; Walker, Brakefield, Hobson, & Stickgold, 2003). Researchers have postulated that the neural activity of the consolidation process can be disrupted if the same areas of

activation are utilized to learn a second, competing task before the consolidation-based stabilization process for a first-learned task is completed (Shadmehr & Brashers-Krug, 1997; Walker, Brakefield, Hobson, & Stickgold, 2003). This competition for consolidation-related processes has been examined in several studies using two similar tasks learned in close proximity. For example, Walker et al. (2003), studying performance on a sequential keypress task, found significant improvement in subjects' task performance of a single novel task 24 hours after initial training. But when subjects learned two very similar tasks (repeatedly pressing the keys 4-1-3-2-4 or 2-3-1-4-2 on a computer keyboard) in a single training session, the first task did not show evidence of overnight enhancement. Similar disruptions of post-training consolidation have been observed in several other studies as well (Dorfberger, Adi-Japha, & Karni, 2007; Fischer, Nitschke, Melchert, Erdmann, & Born, 2005).

At this point, it is important to distinguish among the several meanings of the term interference in the literature. Retroactive interference typically refers to an immediately observable degradation in memory caused by the introduction of a new stimulus (independent of any further consolidation-based processes). For example, after practicing two new skills in juxtaposition, learners sometimes show *immediate* loss of practice-related gains on the skill learned first as a result of having practiced the second skill. Retroactive interference has been studied extensively, and its behavioral manifestations are well characterized.

Interference that is caused by disruption of the consolidation process, however, does not typically cause an observable decrement in the performance of acquired skills, but often blocks the offline gains that develop during overnight sleep. Walker et al. (2003), for example, demonstrated that interference between two novel keypress sequences was not apparent immediately after the sequences had been practiced.

Following an extended practice session in which learners practiced both sequences, immediate retests indicated no performance decrements in the performance of either sequence. Following overnight sleep, however, the sequence learned second showed performance enhancements in accuracy, but the sequence learned first showed no such gains in accuracy overnight. These findings were interpreted as evidence that learning the second sequence interfered with the overnight consolidation of the sequence learned first. When Walker and his colleagues introduced the two sequences in separate practice sessions separated by 6 hours, learners showed overnight consolidation-based gains in the performance accuracy of both sequences.

Duke and Davis (2006) also examined offline learning and interference in unskilled learners using a similar task. Learners in their study experienced delayed overnight gains in performance after practice on a single 5-element keypress sequence; however, when learners practiced two sequences in a single training session (as in Walker et al.), they showed overnight gains in the performance of both sequences.

Although practice of two, similar tasks in a single session has been shown to disrupt the stabilization process of the task learned first, Balas, Roitenberg, Giladi, and Karni (2007), in a more recent study, challenged the assumption that interference occurs only with highly similar tasks in which a "critical overlap" between the tasks' neural representations exists. Balas et al. demonstrated that disruption of consolidation may occur even between two somewhat dissimilar tasks (in this case, between a sequential finger-opposition task and a handwriting task). In addition, Balas et al. demonstrated that task familiarity may play a role in offline consolidation processes, suggesting that a difficult, *familiar* task may be maintained in a more basic, fundamental form in memory, and that this more simple representation can then compete with, and potentially interrupt, the memory for a new simple task. Their subjects all first practiced a simple finger-

opposition sequence task, then immediately practiced one of two complex handwriting tasks (either novel or familiar). The familiar handwriting task, and not the novel task, interfered with subjects' overnight consolidation of the finger-opposition sequence. This finding raises two interesting ideas: that a new skill memory can be affected even by practice on a second, *dissimilar* task, and that familiar and unfamiliar skill memories are processed differentially in the consolidation process.

Recent studies have demonstrated that a learner's age may affect consolidation-based stabilization and enhancement processes as well. Dorfberger, Adi-Japha, and Karni (2007) found that, although adults and children exhibited similar practice-related and overnight gains on a single sequence-learning task, they were affected differently by the introduction of a second, similar sequence following practice. After practice on the second task, 17-year-old subjects demonstrated the expected interference effects upon retest following sleep (exhibiting no significant gains on the task learned first), but the 9- and 12-year old children in the study seemed unaffected—exhibiting significant overnight gains for the task learned first. In other words, motor consolidation in younger children was significantly less susceptible to interference by a second task than was motor consolidation in young adults. These findings raise the possibility that learner age (and perhaps experience) modulate offline learning processes, such that children are either able to consolidate new skill memories faster, or are able to consolidate multiple new memories concurrently.

The phenomenon of memory consolidation has only recently been explored with musicians and musical tasks. In the first study to examine memory consolidation in musicians, Simmons and Duke (2006) demonstrated consolidation-based enhancement effects in skilled musicians practicing a musical task. Subjects practiced a 12-note melody on piano and were then retested following periods of wake or sleep. The results

were the first indication that musicians and musical tasks benefit from memory consolidation following training. However, no study of musicians has yet examined interference during the post-acquisition stabilization period by practice on a second, similar task.

Further research is needed to examine the process of memory consolidation in skilled musicians in the context of musical tasks. This research would not only add to the existing body of literature regarding music practice, but would help to clarify our understanding of the memory consolidation process in skilled learners. A closer examination of consolidation effects in skilled learners would shed light on the memory processes involved in existing memories, or with new memories that are similar to those that are already formed. In addition, the role of auditory perception, processing, and feedback in music practice, and their role in procedural memory consolidation, has not yet been systematically examined.

It is understood that after task practice, the new memory for a motor skill in unskilled learners becomes more stable after approximately 6 hours, rendering it resistant to interference by competing stimuli. Is this effect the same in skilled learners, including musicians? Are new memories still fragile after practice in learners who are accustomed to practicing many different motor tasks in close juxtaposition on a daily basis (e.g., music practice)? For expert learners, would subsequent practice on similar tasks interfere with the consolidation process?

The aim of this study was to examine factors related to memory acquisition and stabilization and the processes underlying music skill learning. Specifically, I focused on sleep's effect on the performance of a musical task, and examined the post-acquisition period following practice by introducing a second musical task. These findings add to our growing knowledge of motor skill acquisition and consolidation, both in skill learning, in

general, and in music learning, in particular. Pursuing these research questions, as well as exploring the relevant research in the fields of neuroscience and psychology, continues to bridge the gap between disciplines, and affords us a better understanding of music and music practice and many aspects of motor skill acquisition and consolidation in skilled learners.

In the experiment described in this document, I sought to answer the following questions:

1. When experienced musicians learn and practice a new musical task, one that includes visual, motor, and auditory components, does the memory for the task show evidence of delayed offline enhancement following overnight sleep?
2. When experienced musicians learn two, similar musical tasks in succession, does learning the second task interfere with the memory of the first task?
3. If so, is the interference effect a result of immediate disruption of the memory for the task learned first (a phenomenon termed retroactive interference), or is it a result of interference during post-training consolidation?

LIMITATIONS OF STUDY

All participants in this study were musicians who volunteered to participate. Participants agreed to get a full night's sleep between our appointments, but I relied upon self-reports of sleep and alertness during sessions. The requirement that participants practice the melodies from beginning to end, without isolating and repeating difficult elements of the task, is unlike typical music practice to which all of the participants had undoubtedly become accustomed. Thus, generalizations of these findings to the typical behavior of musicians should be made cautiously.

II. REVIEW OF LITERATURE

The human brain encounters countless familiar and unfamiliar experiences every day. Whether reading facts, interpreting visual and auditory sensory information, or practicing newly learned skills, learners must process and organize experiences in ways that facilitate future retrieval. Although the neural mechanisms underpinning the organization and storage of new experiences are not yet entirely understood, recent research regarding procedural memory, including motor skill memory, illuminates some of the processes believed to underlie the acquisition of new procedural skills and their subsequent retrieval. The processes involved in learning, traditionally thought to occur only during active practice or exposure to stimuli, are now believed to develop over a much longer time scale, one that begins during practice and continues hours and even days afterward.

INITIAL PRACTICE AND MEMORY ACQUISITION

During initial practice of a novel motor skill, learners generally perform at relatively slow speeds with relatively high error rates as they negotiate the parameters of the task and formulate a cognitive representation of the task. Very soon after, with repetition and continued practice, substantial behavioral improvements in performance are seen as learners make large adjustments to their movements, using kinesthetic, visual, and auditory feedback to gauge and modify performance. The rate of improvement gradually slows as learners refine their performance by making more subtle and fine-tuned adjustments, eventually reaching a point at which no further within-session gains

are possible. The improved performance is typically characterized by faster speed, greater accuracy, and smaller corrective movements.

These improvements during initial task practice typically follow a power curve, with so-called "fast learning" occurring at the beginning and performance gradually reaching asymptote (see Figure 1) (Hauptmann, Reinhart, Brandt, & Karni, 2005; Karni, Meyer, Jezzard, & Adams, 1995; Karni et al., 1998; Korman, Raz, Flash, & Karni, 2003; Walker, Brakefield, Hobson, & Stickgold, 2003).

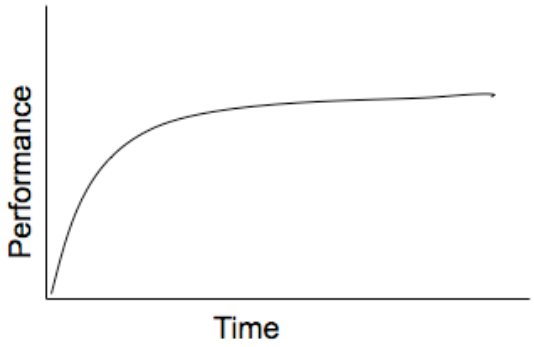

Figure 1. A typical within-session learning curve during practice.

Fast learning, which can occur within minutes and with only a few repetitions, is thought to reflect the creation of a mental representation for the task (Karni, Meyer, Jezzard, & Adams, 1995; Karni et al., 1998). The time in fast learning may be too brief for extensive structural changes to occur in the brain, and may simply allow for a "tagging" of synapses that later develop further, more lasting changes (Walker, 2005). Following fast learning during practice, however, a period of "slow learning" begins and continues following practice.

In addition to behavioral improvements that are readily observable during initial practice, areas of brain activation change during practice as well (Doyon, Ungerleider, Squire, & Schacter, 2002; Hund-Georgiadis & Yves von Cramon, 1999; Karni, Meyer,

Jezzard, & Adams, 1995; Kelly & Garavan, 2005; Petersen, Van Mier, Fiez, & Raichle, 1998). Motor skill practice is known to initially involve the cerebellum, basal ganglia, and motor cortices (Ashe, Lungu, Basford, & Lu, 2006; Doyon et al., 2002; Grafton et al., 1992; Graybiel, 1995; Lehericy et al., 2005; Mueller, Kleinhaus, Pierce, Kemmotsu, & Courchesne, 2002; Penhune & Doyon, 2002; Savion-Lemieux & Penhune, 2005; Van Mier, Perlmutter, & Petersen, 2004). Although somewhat dependent upon the nature of the task, these areas of activation typically change with continued training to involve different locations. For example, Grafton et al. (1992), using neuroimaging techniques, found that neuronal activity during early practice on a motor coordination task led to increases in activations in the left motor cortex, the left supplementary motor area, and the thalamus, locations that represent a subset of the neuronal network where such hand/arm behavior generally exists.

Peterson, van Mier, Fiez, and Raichle (1998) propose a "scaffolding-storage" framework to explain changes in practice-related blood flow. They suggest that for "unskilled, effortful performance, a scaffolding set of regions is used to cope with novel task demands. Following practice, a different set of regions is used, possibly representing storage of particular associations or capabilities that allow for skilled performance" (p. 853).

Several studies have demonstrated that continued skill practice results in a general shift from cortico-cerebellar networks to cortico-striatal networks. This is believed to represent a shift in the location where the procedural memory is maintained (Doyon & Benali, 2005; Doyon et al., 2002; Peigneux et al., 2006), or a shift from feedback- to feedforward-controlled execution, representing increased automaticity (Puttemans, Wenderoth, & Swinnen, 2005). Activation seen in areas supporting attention and control

tend to drop off following early practice as well, as learners become familiar with the task (Kelly & Garavan, 2005).

With additional practice, the size of the activation in cortical motor areas changes in a manner that is specific to the effectors involved in task performance (Karni, Meyer, Jezzard, & Adams, 1995). For example, in a study by Classen et al. (1998), as little as 15 minutes of practice (in a single session) on a unidirectional thumb movement task evinced changes in the area of the cortical network representing the thumb. In another example, using a piano task, the size of activation in areas representing the specific fingers utilized in the task increased over time with practice (Pascual-Leone, Dang, Cohen, Brasil-Neto, & Hallett, 1995). Activation in these areas increased significantly with practice on a piano melody over a 5-day period, whereas subjects practicing random notes for the same period of time exhibited no changes in neural activation. This may indicate that the cortical representation for a specific body part increases preferentially with practice, especially when movements have a functional significance. For example, Elbert el al. (1995) found that string players' left hand finger representations are much larger than those of nonmusicians. Karni et al. (1998) also observed a more extensive representation of subjects' fingers following 3 weeks of daily practice on a finger opposition task.

MEMORY STABILIZATION FOLLOWING PRACTICE

Research on the neural substrates of skill learning indicates that the underlying cortical reorganization that begins during physical practice also continues in the hours after the cessation of practice. During this time, skill performance levels are typically maintained, but continuing changes in the brain following initial practice of novel skills

are thought to stabilize the new memories, rendering them less vulnerable to interference by competing stimuli (Walker et al., 2003). This process, termed *consolidation-based stabilization*, begins during active practice and continues across subsequent hours, with the new memories becoming more resistant to interference during the 4 to 6 hours after practice has ended (Brashers-Krug, Shadmehr, & Bizzi, 1996; Duke & Davis, 2006; Fischer, Hallschmid, Elsner, & Born, 2002; Shadmehr & Holcomb, 1997; Walker, Brakefield, Hobson, & Stickgold, 2003).

Abel and Lattal (2001) assert that the initial acquisition and subsequent stabilization of new procedural memories share many of the same molecular mechanisms. These neural processes begin as a direct response to stimuli during skill acquisition, but continue in the absence of stimuli following practice. For example, Peigneux and his colleagues (2006) observed continuing neural activity after practice in the same cerebellar-cortical and striatal-cortical networks that were observed during early and late physical practice on a serial-reaction time task. It seems probable that the brain cannot create all of the considerable neurochemical and neurophysiological changes necessary to fully store and integrate new memories in the moment, so it must continue these modifications later. Of course, it would be disadvantageous to retain and remember everything encountered, and time (and further repetitions) serve to filter which information and skills are preserved and integrated into existing memory, and which are not.

The period following practice involves physical changes in the brain, including the synthesis of new proteins and changes in long-term potentiation. Long-term potentiation, the reduction in the amount of energy needed to trigger various synaptic circuits, is one of the most fundamental molecular components of learning, although it is not fully understood. Long-term potentiation and its opposite, long-term depression, are

thought to work together to regulate synaptic networks for learned behavior (Walker, 2005). Chemical changes involved in long-term potentiation, such as the reduction in concentration of the neurotransmitter gamma amino butyric acid (GABA) and an increase in the neurotransmitter acetylcholine, occur following practice and have been implicated in increased brain plasticity and neocortical reorganization (Butefisch et al., 2004; Floyer-Lea, Wylezinska, Kincses, & Matthews, 2006).

It is thought that behavioral gains from active practice are simply maintained during the period of post-training wake (Walker, Brakefield, Hobson, & Stickgold, 2003; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Walker et al., 2003), although several recent studies indicate that perhaps performance changes can occur over this time as well. For example, Hotermans, Peigneux, Noordhout, Moonen, and Maquet (2006) found that subjects demonstrated a performance "boost" on a keypress task when tested 5 to 30 minutes after training. Simmons (2007) found similar gains using a musical task, with some subjects showing performance improvements across 6 hours of post-training wake. Davis (2007), using a keypress task, found subjects' performance was significantly improved after taking a five-minute rest break during early practice. Davis suggests that a break during the fast learning stage of early practice afforded an opportunity for offline processes to begin. These underlying processes, which are typically believed to initiate during the slow learning phase of active practice, could possibly begin during a break in practice, which Davis refers to as a possible "pre-consolidation" phase. It could also be the case that a rest break provides a relief of the buildup of practice-induced inhibition, as suggested by Walker (2005).

INTERFERING WITH THE STABILIZATION PROCESS

Researchers have been able to examine the period of consolidation-based stabilization, in which memories move from labile to a more stabile state following practice, by introducing interfering stimuli during this period. The neural changes that continue across wake following active practice can be disrupted by these stimuli; the magnitude and timeline of disruption has illuminated much about the mechanisms involved in procedural learning and memory, and have led to the formation of theories on the neural underpinnings of learning (McGaugh, 2000; Walker, 2005; Walker & Stickgold, 2006).

For example, applying transcranial magnetic stimulation (rTMS) over the primary motor cortex immediately following training has been shown to impair subsequent memory consolidation and performance (Baraduc, Lang, Rothwell, & Wolpert, 2004; Muellbacher et al., 2002; Robertson, Press, & Pascual-Leone, 2005). This noninvasive process sends repetitive magnetic pulses to excite neurons at specified locations in the brain, which can in turn modulate brain activity. Although rTMS applied to the motor cortex immediately after practice on a novel motor skill can disrupt subsequent offline gains, applying rTMS to the same location 6 hours after training results in no decrement in overnight consolidation. This finding seems to indicate that during this 6-hour period following training, the memory is processed in such a way that it becomes less susceptible to interference in the motor cortex (Muellbacher et al., 2002).

It has more recently been demonstrated that learning two novel tasks in succession can similarly disrupt offline gains in performance, reducing or eliminating the consolidation-based enhancement effects that would typically be observed in the performance of the first novel task following sleep (Brashers-Krug, Shadmehr, & Bizzi,

1996; Dorfberger, Adi-Japha, & Karni, 2007; Shadmehr & Brashers-Krug, 1997; Walker, Brakefield, Hobson, & Stickgold, 2003). It is important to note that this only eliminates the expected subsequent *offline* gains, and not the performance gains obtained from active practice itself.

For example, Walker et al. (2003), studying performance on a sequential keypress task, found that when subjects learned two tasks in a single training session, they showed improvement in accuracy after sleep only on the sequence learned second. In order to rule out the possibility that learning a second task immediately interfered with the memory of the first task, another group of subjects learned the same two tasks, but were retested on the first task immediately after learning the second task (rather than after sleep). These subjects showed no immediate decrement in speed or accuracy at the end of training, indicating that the interference seen after 24 hours occurred during the posttraining consolidation period, and not during the actual practice of the second task itself. However, Duke and Davis (2006), using a keypress task identical to that used by Walker et al., did observe overnight gains in the task learned first, although not as great as the gains observed for the second task.

Several researchers have offered hypotheses to explain why a learned task might disrupt the consolidation process for another, similar task. Fonseca, Nägerl, Morris, and Bonhoeffer (2004) propose that learning two similar tasks in close proximity causes competition between synapses for the same proteins necessary for plasticity—a phenomenon they refer to as "competitive maintenance." Balas et al. (2007) attribute it to a "representational overlap," recently demonstrating that a familiar, though dissimilar, task (handwriting) can interfere with a novel task (in this case, a finger-opposition task). Balas et al. proposed that even dissimilar tasks can compete for the brain's resources following practice and suggest that complex but well-practiced movement sequences may

come to be represented as simpler ones in long-term motor memory, and that this "representational overlap" is what causes the behavioral interference. Balas et al. assert that this overlap "may result in the weakening or even the taking over of ongoing neuronal consolidation processes, triggered by the initial training experience, by the subsequent experience" (p. 500). Dorfberger and his colleagues (2007) have recently proposed that in adults, the memory consolidation process is mediated by a "recency" effect, and that "in situations of multiple, clashing experiences occurring within a short time-interval, adults may less effectively establish in memory experiences superseded by newer ones" (p. 1).

Although several studies have determined that a memory for a new procedural skill is stable and resistant to interference 4-6 hours following practice, researchers do not yet have a clear timeline of events during the hours following practice leading up to this stabilization. In an early study of motor memory consolidation, Jerusalinsky et al. (1994) found that injecting a protein kinase C (PKC) inhibitor into the rat brain within two hours of learning interfered with subsequent memory formation and consolidation. Brashers-Krug et al. (1996) found, using a force field task with humans, that teaching a second task 5 minutes or 1 hour after practice on a first task interfered with consolidation of the first task, but not if the task was introduced after a period of 4 hours following practice on the first task.

Offline gains were evident in Shadmehr and Brashers-Krug's (1997) study when subjects learned a second task 5.5 hours after practice on a first task, but not when the second task was learned only 5 minutes, 30 minutes, or 2.5 hours after learning the first task. In a study using sequential keypress tasks, Dorfberger, Adi-Japha, and Karni (2007) showed that introducing a second task 2 hours after first-task practice interfered with memory consolidation in adults, but, interestingly, not in 9- and 12-year old children.

Although the children and adults showed comparable overnight gains when only one sequential keypress task was practiced in a single session, the introduction of a second, similar task two hours after training interfered with subsequent offline gains only in the adults, and not in the children. In other words, a second competing task introduced two hours after initial practice on a first task had no adverse effect on children's consolidation. The authors suggest that children either stabilize new memories on a faster timeline than adults (such as within the two hours in this study), or are capable of consolidating multiple new memories concurrently with no detrimental effects to either memory's consolidation.

In a previous study, I found that several different tasks interfered with skilled learners' performance of a piano melody following sleep (Allen & Duke, 2007). Participants, all musicians, practiced a 9-note piano melody with their nondominant hand, and then either learned a second piano melody, learned a new piece on their principal instrument, practiced a familiar piece on their principal instrument, or engaged in no other music-related motor behavior prior to sleep. All subjects returned the following morning to be retested on the original piano melody. Results indicated that learning a novel melody on subjects' primary instrument had the greatest interference on overnight memory consolidation for the task learned first. This finding contradicts the finding by Balas et al. (2007) of the greatest interference by a complex, familiar task, and more research is necessary to explain this apparent discrepancy.

It is important to clarify at this point that the type of consolidation-based interference discussed here is distinctly different from *retroactive* interference (also called *retroactive* or *retrograde amnesia*) discussed in learning literature (Miall, Jenkinson, & Kulkarni, 2004; Misanin, Miller, & Lewis, 1968; Riccio, Millin, & Gisquet-Verrier, 2003). "Interference" in the memory consolidation literature refers only to the

disruption of the consolidation process and diminution of the subsequent offline gains that would otherwise be expected overnight, leaving acquisition gains intact. However, "retroactive interference" typically refers to phenomena in which acquisition-based performance gains are actually degraded, an effect that is visible immediately after the introduction of the competing stimuli, such as practice of a second similar task.

Interference in motor tasks has been frequently studied using motor adaptation tasks, which typically involve the manipulation of a lever against a varying force field. However, these tasks produce results conflicting with many keypress or sequence-learning tasks, as motor adaptation memories do not seem to consolidate in the same way or respond the same way to interfering tasks (Doyon & Benali, 2005). Such motor adaptation tasks rely upon subjects' responses to kinesthetic feedback throughout task practice; they must adapt to constantly changing forces, manipulated by the experimenter, as they move. Furthermore, depending on the dynamics of experimental force fields, a given movement may obtain different response outcomes. In other words, unlike sequence learning tasks, in which a given movement produces a consistent result, motor adaptation tasks do not associate one movement with a consistent result; the same movement produces a varying response, out of the learner's control, to which he or she must then adapt.

SLEEP-BASED MEMORY CONSOLIDATION

Although new procedural memories are stabilized in the hours of wakefulness following physical practice, the process of memory consolidation continues during sleep in a process referred to as *consolidation-based enhancement*. During the period of overnight sleep following practice, further memory refinements continue in the brain, resulting in enhanced skill performance after sleep (Brashers-Krug, Shadmehr, & Bizzi,

1996; Cohen, Pascual-Leone, Press, & Robertson, 2005; Korman, Raz, Flash, & Karni, 2003; Stickgold, Whidbee, Schirmer, Patel, & Hobson, 2000; Walker *et al.*, 2003); some motor skills even show behavioral improvements following a 90-minute nap (Mednick, Nakayama, & Stickgold, 2003). The same skills do not improve over comparable durations of wake, which seems to indicate that sleep plays a specific role in the consolidation-based enhancement process (Fischer, Nitschke, Melchert, Erdmann, & Born, 2005; Walker, Stickgold, Alsop, Gaab, & Schlaug, 2005). Typically, performance following sleep is more even, faster, and more accurate than performance before sleep (Dorfberger, Adi-Japha, & Karni, 2007; Kuriyama, Stickgold, & Walker, 2004; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002). These posttraining changes have been termed "offline" learning (Karni et al., 1998). However, offline learning is also sometimes referred to as "slow" learning; it is important to distinguish between slow learning after the cessation of practice and the slow learning phase during active practice itself.

Although sleep-based performance enhancements are greatest following the first night of posttraining sleep, several studies provide evidence that further enhancement continues across several days (Atienza, Cantero, & Dominguez-Marin, 2002; Atienza, Cantero, & Stickgold, 2004; Duke & Davis, 2006; Stickgold, James, & Hobson, 2000). Duke and Davis (2006), using a sequential keypress task, found additional offline enhancements over a second night of sleep. Walker et al. (2003), using a similar keypress task, observed greater offline gains when subjects were tested 3 days, rather than 1 day, after training. Stickgold, James, and Hobson's (2000) study of visual discrimination showed subjects' continued improvement, absent additional practice, for up to four days, reaching maximal improvement 48-96 hours after the end of training. After this, no

further enhancement was observed, perhaps evidence that the limits of sleep-based improvements had been reached.

Recent research using fMRI data has confirmed that the brain undergoes sleep-dependent neurophysical changes following motor learning. Fischer et al. (2005) reported that differences in neural activation between performance at training and retest were only evident if the retest followed a period of sleep. It has been proposed that this difference in activation after sleep signifies a change in the underlying anatomical representation of the motor task, as well as the translocation of the memory to a different site (Fischer, Nitschke, Melchert, Erdmann, & Born, 2005; Walker, Stickgold, Alsop, Gaab, & Schlaug, 2005). It is unclear as to whether this "translocation" of a memory occurs exclusively over sleep or may occur over wake as well.

In one example, Walker, Brakefield, Morgan, Hobson, and Stickgold (2002), using an fMRI procedure during training and retest on a sequential finger-tapping task, found increased activation following sleep in areas previously linked to error monitoring (cerebellum), planning motor sequences, and optimizing difficult transitions (anterior medial prefrontal cortex). In the same study, reduced activation found in fronto-polar areas during practice following sleep indicated a reduced need for online monitoring of skills, improved task automation, and reduced activation in areas associated with the limbic system, all of which indicates a greater ease of task performance. Learners who did not sleep between training and retest sessions did not exhibit these changes.

Similar results have been found using a finger-opposition sequence-tapping task (Fischer, Nitschke, Melchert, Erdmann, & Born, 2005). After posttraining sleep, subjects showed reduced activation in prefrontal, primary motor, and premotor areas of the brain during practice, although subjects who were deprived of sleep on the first posttraining night exhibited no changes in brain activation between training and retest, even after 48

hours and additional recovery sleep. Subjects who had post-training sleep exhibited improvements in speed and accuracy, whereas subjects who did not sleep the first night posttraining made no further gains, even after recovery sleep. Fischer and his colleagues postulate that the reduced activation following the first night of sleep may indicate that during this sleep, the brain eliminates information that is unnecessary for optimal performance. Thus, the decreased areas of activation following sleep could represent a more "efficient" skill representation in the brain.

Several researchers have suggested that the sleep-based consolidation process is triggered when an asymptotic level of performance improvement is reached during initial practice, and that practice not reaching an asymptotic level either fails to trigger sleep-based consolidation (Hauptmann, Reinhart, Brandt, & Karni, 2005; Karni et al., 1998; Korman, Raz, Flash, & Karni, 2003) or delays any observable consolidation effects (Hauptmann & Karni, 2002). In a study by Hauptmann et al. (2002), subjects who practiced 3 blocks on a letter enumeration task did not demonstrate the significant overnight gains that were obtained by other subjects who practiced for 10 blocks on the same task, but did show gains following the *second* night of sleep. This suggests that the time scale of overnight consolidation may be related to the degree of improvement achieved during initial skill practice; skills whose rates of improvement fail to reach asymptote in a training session may consolidate more slowly and over the course of several nights than may skills whose rates of improvement reach asymptote during training.

Once an asymptotic of task performance is attained during practice, further practice does not seem to increase the magnitude of overnight gains. Doubling the amount of practice during initial training (beyond the leveling off of performance gains) does not necessarily increase the benefits of consolidation-based enhancement (Savion-

Lemieux & Penhune, 2005; Walker et al., 2003). Hauptmann and his colleagues (Hauptmann & Karni, 2002; Hauptmann, Reinhart, Brandt, & Karni, 2005) have suggested that reaching an asymptotic level of performance during practice is necessary to trigger further offline gains. It has not yet been determined if this is the case, nor has it been determined whether additional practice, after a level of automaticity has been reached, has other consolidation benefits, such as making a memory less susceptible to post-training interference.

Not all aspects of motor sequences are enhanced equally during sleep. Using a sequential keypress task, Kuriyama and his colleagues (2004) observed that performance improvements following sleep were due primarily to improvements in the most difficult transitions between elements of the sequence, the "problem-points" (see Figure 2).

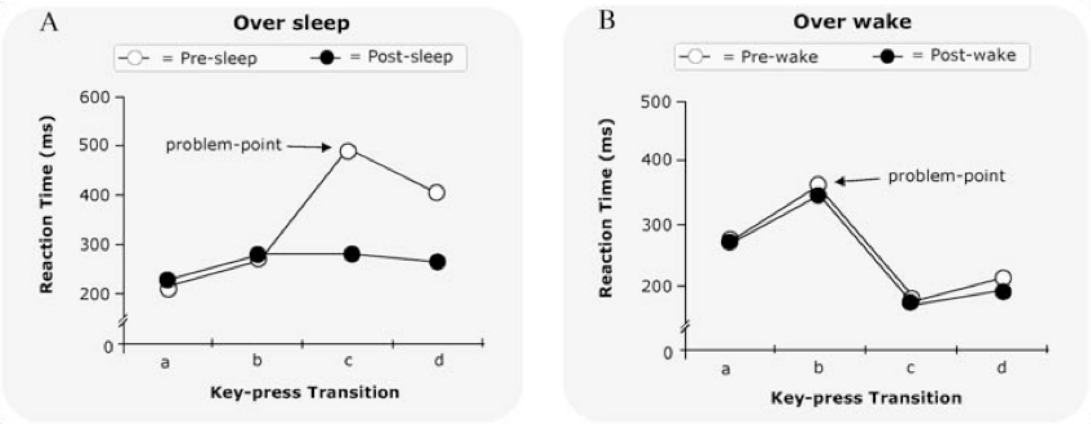

Figure 2. Individual subjects' pre- and post-test performances of a 5-element sequence, over periods either with or without sleep (Kuriyama, Stickgold, & Walker, 2004, p. 710).

The authors also found that subjects who practiced a 9-element sequence exhibited greater benefits of sleep-based consolidation than did subjects who practiced a shorter, 5-

element sequence (as the longer sequence length adds more transitions). Kuriyama et al. suggest that the sleep-dependent learning process benefits the aspects of motor learning that are most difficult prior to sleep.

In light of the results supporting sleep-based consolidation, what function does sleep serve that cannot be achieved during equivalent time awake? It is important here to clarify that sleep is not a homogeneous state, but rather a cyclic repetition of sleep stages. Human sleep has been categorized into two main types: rapid eye movement (REM) sleep and non-rapid eye movement (NREM) sleep. NREM sleep comprises four stages, with Stage 4 NREM sleep being the deepest stage of sleep (see Figure 5). Stage 3 and 4 NREM are also often referred to as "slow wave sleep" or SWS.

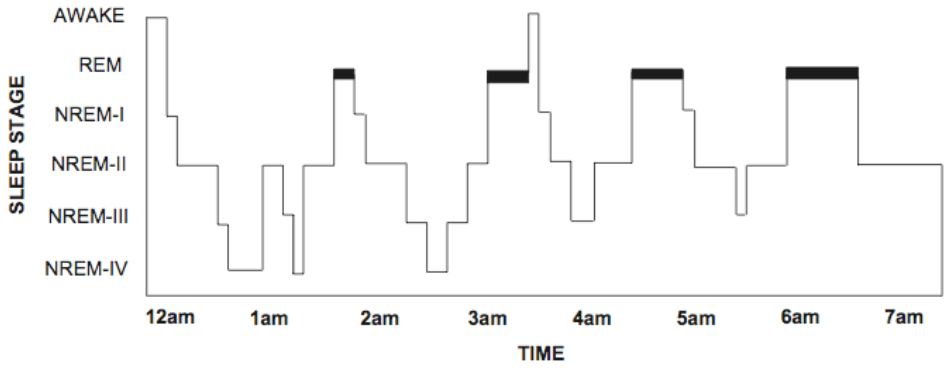

Figure 3. The stages of human sleep, including REM (rapid eye movement) and non-rapid eye movement (NREM) sleep (Walker, 2005, p. 52). The dark bars represent REM sleep.

The average person takes around 90 minutes to cycle through all of the sleep stages, although the ratio of REM to NREM within each cycle may vary. Slow wave sleep typically dominates early in the night, and REM and Stage 2 NREM become more prevalent later in the night. The exact purpose of these sleep stages is unknown, but many

researchers believe either that REM and NREM sleep each handle different types of memory, or that the sleep stages form a complementary cycle of processes that work together in sequence.

Ellenbogen, Payne, and Stickgold (2006) recently outlined four major prevailing positions on sleep's role in memory consolidation. Although they specifically address declarative memory in their article, the same line of reasoning can be applied to procedural memory consolidation as well. The four points of view that they outline are: 1) sleep contributes nothing to memory; 2) sleep transiently shelters memories from interference; 3) sleep creates conditions conducive to memory consolidation, but plays no other unique role in the consolidation process; and 4) unique properties of sleep are directly involved in the memory consolidation process. They conclude that "although the precise causal mechanisms within sleep that result in memory consolidation remain elusive, recent evidence leads us to conclude that unique neurobiological processes within sleep actively enhance" memories (p. 716).

Of course, several additional proposed theories exist to explain sleep's role in motor memory consolidation. For example, Vertes and Eastman (Vertes & Eastman, 2000) aver that it is the *declarative* component of any task that is sleep-dependent. Almost every "procedural" task has at least a small declarative component (e.g., being able to verbalize the sequence in a finger-tapping task), and this may explain why tasks that are implicit (i.e., learned without awareness) and involve very little declarative knowledge have been found to improve over wake, independent of sleep (Robertson, Press, & Pascual-Leone, 2005).

A recent study examining this same implicit/explicit proposition has successfully shown that "interrupting" the declarative component of an explicit motor task (by forcing practice on a competing declarative task) can induce offline improvements over wake as

well (Brown & Robertson, 2007). In this study, subjects were trained in a serial-reaction time task (SRTT), a popular experimental procedure in the study of implicit memory. In this task, subjects respond to cues on a computer screen by pressing corresponding keys on a keyboard; unbeknownst to the subjects, a repeated sequence is imbedded within series of key presses. Better performance by subjects on this sequence, as compared to performance on other, randomly ordered elements in the series, reflects subjects' implicit learning of the sequence. Brown and Robertson alerted subjects to the presence of an imbedded sequence, thus making this typically implicit task somewhat more explicit. Immediately after training, subjects either learned a word list or participated in another cognitively demanding second task: 12 hours later they were retested on the original SRTT. The subjects who learned the declarative word task exhibited off-line performance improvements over the day, which the authors attribute to the "disruption" of the consolidation on the declarative component of the SRTT (Robertson, Pascual-Leone, & Press, 2004). This finding could support the assertion by Vertes and Eastman that the declarative component of a task requires sleep to produce offline enhancements; disrupting the declarative component can induce offline improvements over wake. Further research is needed to explore this finding.

It has also been proposed that initial training produces *multiple* representations of a task (e.g., the physical movement, the goal) in the brain, each encoding different dimensions of the task simultaneously, and that these dimensions may be enhanced differentially. Cohen et al. (2005) have suggested that different circuitry in the brain governs *goal*-based and *movement*-based learning. By testing the same SRTT sequences with subjects' trained and untrained hands, these researchers were able to compare offline improvements, and observed that sleep helps to consolidate goal-based learning, rather than movement-based learning. In further support of this idea, Robertson et al. (2005)

found that neural circuitry commonly associated with goal-based learning is preferentially activated during sleep, whereas the movement-based areas of the brain, such as the primary and supplementary motor cortexes, are more engaged during post-training wake.

In an interesting, if perhaps not widely-held, theory on the role of sleep stages in memory consolidation, Smith has proposed that it may not be the *nature* of the task (e.g., motor, perceptual, declarative) that affects its sleep-dependence, but the *familiarity* of the task (2005). He suggests that familiar and unfamiliar information and skills are processed during separate sleep stages, with REM mediating novel material and NREM mediating familiar material and associations. Familiar tasks, such as pressing a key on a computer keyboard are "simply refining existing programs and do not need to devise new strategies," and therefore benefit most from NREM sleep. Newborns, in contrast, must create new strategies for almost every stimulus they encounter because *all* is new, which according to Smith would explain their larger proportion of sleep time devoted to REM sleep compared to adults. With this theory, much of memory consolidation depends on the experience and sophistication of the learner. Smith's ideas are fascinating in that they include a more developmental view of sleep's role, and certainly warrant further research.

A number of researchers have proposed a link between offline performance gains and Stage 2 NREM sleep. Walker and his colleagues (2002) reported a significant correlation between subjects' overnight improvement in speed on a sequential keypress task and their amount of Stage 2 NREM sleep in the last quarter of the night. In fact, this correlation was so strong that it accounted for 52% of the variance in retest performance. This strong Stage 2 connection is further supported by Fogel, Jacob, and Smith (2001), who found that the amount of time subjects spent in Stage-2 NREM sleep increased following training on a motor task. Similarly, Smith and MacNeill (1994) reported the

elimination of expected offline gains when subjects were deprived of Stage-2 sleep following training on a pursuit-rotor task (while REM deprivation did not affect overnight gains).

Stage 2 NREM sleep is known to contain a high frequency of *sleep spindles*, brief bursts of neuronal firings that are speculated to be involved in synaptic plasticity. The frequency of these sleep spindles in Stage 2 NREM sleep has been found to increase by up to 40% following intensive motor skill practice, further linking this sleep stage with motor learning (Fogel, Jacob, & Smith, 2001; Fogel & Smith, 2006). Although the exact function of NREM sleep remains unclear, it seems related to the sleep-based enhancement of motor skills.

There is ample evidence implicating REM sleep in procedural memory consolidation as well. Karni, Tanne, Rubenstein, and Askenasy (1994) found that REM sleep deprivation on a visual texture-discrimination skill prevented sleep-based enhancement. Using an SRTT task, Maquet et al. (2000) and Peigneux et al. (2003) found that subjects experienced brain reactivations during REM sleep that resembled those of practice; subjects who achieved higher performance levels in practice exhibited more reactivation during sleep. However, researchers who argue against the necessity of REM in consolidation cite the absence of any report of memory deficits among patients taking monoamine oxidase inhibitors (MAOIs), drugs which are known to eliminate REM sleep entirely (Siegel, 2005).

Another possibility is that REM and NREM sleep play complementary roles in the memory consolidation process. Stickgold, James, and Hobson (2000) reported that performance enhancements on a visual-perceptual task were correlated with both the amount of slow wave sleep in the first quarter of the night and the amount of REM in the last quarter of the night. In a different study, daytime naps taken after the same visual

task only improved performance when they contained both SWS and REM sleep (Mednick, Nakayama, & Stickgold, 2003). Gais et al. (2000) has proposed that early slow wave sleep initiates the sleep-based consolidation process, and late REM sleep subsequently enhances the memory.

EFFECTS OF EXPERIMENTAL TASK TYPE ON MEMORY CONSOLIDATION

Identifying general trends in the body of memory consolidation research poses some difficulty. The experimental tasks and dependent measures used in these studies are quite diverse, making direct comparisons among results difficult. Even dividing this body of research into clear categories of declarative and procedural memory is difficult, as most procedural tasks contain declarative components as well. For example, in a very common "procedural" task, the sequential finger-tapping task, subjects press a given sequence of numbers repeatedly on a computer keyboard. This task includes both declarative and procedural elements, as subjects not only execute the movement sequence, but also learn this sequence explicitly in that they can verbalize the components of the sequence. Because declarative and procedural tasks are known to engage different memory systems (for a review, see Walker & Stickgold, 2004), understanding the dimensions of experimental tasks is important if one is to meaningfully interpret experimental results.

In fact, much of the disagreement about sleep's precise function in the learning process stems from seemingly inconsistent and contradictory data in the extant literature, particularly data indicating that sleep is not necessary to show consolidation-based enhancement. Some procedural tasks, including implicit motor tasks (Robertson, Press, & Pascual-Leone, 2005), motor adaptation tasks (Caithness et al., 2004), and reaching tasks

(Donchin, Sawaki, Madupu, Cohen, & Shadmehr, 2002) have shown different results, including offline gains over wake.

Research has shown that the nature of the task presentation, specifically learners' awareness of the goal or target stimuli during practice, affects subsequent memory consolidation. Several studies have shown that tasks learned implicitly are consolidated over a different time course than are those learned explicitly. Implicit tasks, such as the SRTT, show consolidation-based enhancements over periods of daytime wake, while explicitly learned tasks require a period sleep for consolidation based enhancement to occur (Born & Wagner, 2004; Robertson, Pascual-Leone, & Press, 2004; Robertson, Press, & Pascual-Leone, 2005). By comparing performance on the SRTT and an explicit version of the SRTT (in which subjects are made aware of the existence of an embedded sequence), researchers have been able to examine differences in offline gains. This subtle difference in methodology yields significant differences in terms of consolidation effects—the implicit version improves over wake, and the explicit version requires sleep.

It is also probable that other aspects of experimental tasks, such as attentional focus, affect performance and learning and should therefore be taken into account when interpreting results. The differential effects of learners' attentional focus on motor task learning and performance have been examined in a variety of contexts (e.g., Wulf & Prinz, 2001), but the effects on the subsequent memory consolidation process has not yet been examined. It is likely that the element of a task to which the learner most attends affects the encoding, organization, and subsequent retrieval of the memory for that task, although this has not yet been addressed or explored in memory consolidation research.

MEMORY RETRIEVAL

Once a memory is encoded and stored, its usefulness depends on its retrievability. Walker and his colleagues have proposed that memories, especially relatively recent memories, reenter a labile state each time they are recalled, requiring an additional consolidation period, or *reconsolidation*, to remain a more or less permanent part of memory (Walker & Stickgold, 2006). Walker et al. (2003) demonstrated that learning a new skill after even briefly recalling a learned skill interfered with the skill learned first, erasing previous offline gains for the first-learned skill.

Memory reconsolidation has been well documented in animal studies (for reviews, see Meeter & Murre, 2004; Sara, 2000), which show that recalling a consolidated memory seems to return it to a labile state, making it vulnerable to interference by electroconvulsive shock, lesions, or the injection of specific chemical agents (such as protein synthesis inhibitors). Przybyslawski, Roullet, and Sara (1999), for example, discovered that when a consolidation-blocking agent, propranolol, was administered to rats within 2 hours of recalling of a learned fear response, the rats showed memory decrements 24 hours later. Rats that received the same injections 5 hours after recall or that received the propranolol without memory reactivation showed no memory deficits. Suzuki et al. (2004), using the same task, showed that rats' stronger fear memories were more stable and resistant to disruption. In addition, older memories (8 weeks after learning) were also found to be more resistant to disruption than were newer memories.

It is clear that memory retrieval is not a passive process. Memory reconsolidation after retrieval seems to be a mechanism used to integrate updated information into long-term, previously consolidated memories (Rodriguez-Ortiz, De la Cruz, Gutierrez, & Bermudez-Rattoni, 2005). Whether or not this process of reconsolidation occurs in

humans, or how extensively and under what circumstances, is not yet clear. In daily life, important memories must be readily retrievable, modifiable, and able to integrate new, useful information, but research with humans has not yet explored this latter aspect of memory storage and retrieval. This area of research is particularly germane to experienced and highly skilled learners, like musicians, who regularly practice and refine well known skills.

MOTOR LEARNING AND MEMORY CONSOLIDATION IN MUSICIANS

Musicians offer a unique and rich subject pool for the study of skill acquisition and refinement, although little is yet known about the mechanisms underlying these processes in musicians. In fact, it is common in motor learning research for musicians to be specifically excluded from the subject pool (e.g., Korman, Raz, Flash, & Karni, 2003).

It is now understood that musicians' brains are both functionally and anatomically different from those of nonmusicians (Pantev, Engelien, Candia, & Elbert, 2001; Schlaug, 2001); however, it is unknown how these differences affect memory consolidation, if at all. Because these structural differences are mainly a result of training, and because neural activation during musical activities differs between musicians and nonmusicians, it may be that memory formation and consolidation differ between musicians and nonmusicians as well.

Study of the acquisition and consolidation of musical tasks poses additional challenges. First, the presence of auditory feedback in music performance adds an additional task dimension. This auditory feedback not only guides learners' behavior and is inextricably linked to music performance, but is also known to engage the auditory cortex, an area of the brain previously unstudied in relation to memory consolidation.

This certainly adds a level of complexity to the analysis of learning and memory with a musical task.

Furthermore, musical tasks are quite complex, in contrast to the simple motor skills typically studied in the existing literature. The types of movements used in music afford the learner many degrees of freedom in performance—which of many keys to press (in the case of a simple piano melody), which combinations of keys to press together (in a more complex melody), how to synchronize these movements together in time to create a rhythm, how to read the notes from written music, and, in the case of many musical instruments, how to *create* the sound (e.g., striking a key, blowing air, drawing a bow across strings). Analysis of music performance thus not only includes examining the dimensions of note speed and accuracy, but also considering the synchrony of movements (rhythm), evenness and speed of pulse (tempo), and volume.

CONCLUSION

Although the exact neural mechanisms and the time course of memory consolidation remain unclear, the effects of consolidation are evident, characterized not only by enhanced performance over time, but also increased resistance to interference by new stimuli. The time course of making memories more or less permanent is not yet fully understood, and certainly depends on many other factors, including complexity and type of task, skill of the learner, amount and type of practice, and performance level achieved during training.

III. METHOD

Procedural skill learning involves both the behavioral and neurological changes that occur during and following active practice, as the brain transforms memories from labile to more permanent states. This process, termed *memory consolidation,* is known to occur during wake and during sleep following practice. Research in psychology and neuroscience demonstrates that new implicit, procedural memories stabilize during the hours immediately following practice and that the subsequent period of sleep often results in performance gains that develop offline. However, during the wake-based stabilization period, which extends for up to 6 hours following practice, other competing stimuli can interfere with new, labile memories, even hindering later sleep-based enhancement that might otherwise occur.

Walker et al. (2003) have shown, using a sequential keypress task, that a recently learned sequence may be susceptible during this period to interference caused by practice on a similar sequence. Although several explanations have been offered to explain this effect, the exact neural mechanisms underlying the phenomenon are unknown, and are only recently being explored more systematically (Balas, Netser, Giladi, & Karni, 2007; Dorfberger, Adi-Japha, & Karni, 2007; Duke & Davis, 2006). The process of memory consolidation in *skilled* learners (such as instrumental musicians) has not yet been carefully studied, and many questions about the learning and forming memories for procedural skills remain unanswered.

The purpose of this study was to answer the following questions concerning motor skill consolidation in musicians:

1. When experienced musicians learn and practice a new musical task, one that includes visual, motor, and auditory components, does the memory for the task show evidence of delayed offline enhancement following overnight sleep?
2. When experienced musicians learn two, similar musical tasks in succession, does learning the second task interfere with the memory of the first task?
3. If so, is the interference effect a result of immediate disruption of the memory for the task learned first (a phenomenon termed *retroactive interference*), or is it a result of interference during post-training consolidation?

PARTICIPANTS

Participants were 60 right-handed male (n = 36) and female music majors enrolled in undergraduate and graduate degree programs at The University of Texas at Austin (age, M = 25.20 years, SD = 5.01). All had completed no more than four semesters of undergraduate group piano instruction and had taken no more than three years of private piano instruction. No participant was enrolled in private piano instruction at the time of the experiment. Participants provided written consent before the experiment (see Appendix A) and were paid $10 for their participation. The Institutional Review Board at The University of Texas at Austin approved the study.

Participants were recruited from music classes at the university. I visited classes to gather names and email addresses of musicians interested in participating and contacted volunteers via email to schedule meeting times. Once 60 subjects had agreed to participate, group assignments were randomly determined.

SETTING, EQUIPMENT, AND SOFTWARE

I met with each participant individually in a quiet room, free of distractions, in the music building at The University of Texas at Austin. Subjects performed on a Roland KR-375 digital piano with full-size, fully weighted keys. The participants and I wore Sony MDR-V150 headphones throughout the experiment.

Software designed specifically for this experiment was written by a computer programmer at The University of Texas at Austin, using Max/MSP software (Puckette & Zicarelli, 2004). Musical Instrument Digital Interface (MIDI) data for the piano performances was recorded on a 12" Apple Powerbook laptop computer using Max/MSP Runtime 4.5 (*Max/MSP*, 2007).

EXPERIMENTAL TASK

Subjects sat at a piano keyboard with the laptop screen visible in front of them (as shown in Figure 4).

Figure 4. Photo of training setting.

They practiced a 13-note melody with their left (nondominant) hand on the piano, using fingerings indicated on the screen. The melody (Figure 5) was adapted from a previous study (Simmons & Duke, 2006). The melody from Simmons and Duke's study comprised two complementary phrases separated by an eighth-note rest. For this experiment I replaced the eighth-note rest with an appropriate pitch so that the melody was a succession of uninterrupted eighth-notes. Performance of the melody required the use of all 5 fingers of the left hand and the repositioning of fingers over different keys; every finger was used for more than one pitch. Music notation and fingerings were visible on the computer screen at all times.

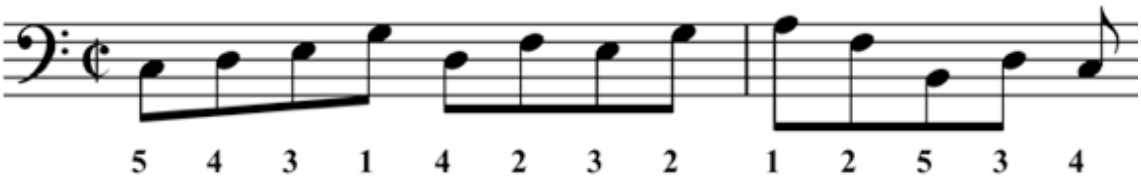

Figure 5. Written notation and fingerings for Melody A.

EXPERIMENTAL GROUPS

I created four groups to test the effects of learning a second melody on the skill memory of the target melody (as outlined in Figure 7). To examine the effect of sleep on skill memory for a single melody, one group practiced only Melody A in the evening and then returned, following sleep, for a brief retest on Melody A (A-SLEEP-a). To examine the effects on consolidation of immediate practice on a second task, another group practiced a second melody (Melody B, see Figure 6) immediately after learning Melody A, and was retested on Melody A following sleep (AB-SLEEP-a).

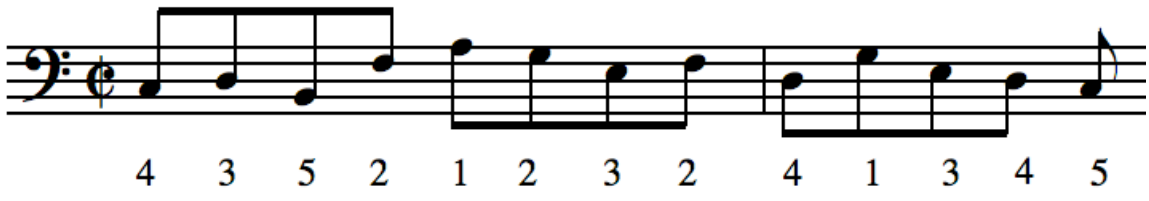

Figure 6. Written notation and fingerings for Melody B.

A third group also practiced Melody A followed by Melody B, but then was briefly retested on Melody A at the end of the evening session as well (ABa-SLEEP-a). This group was also retested on Melody A following sleep. The final group, in order to determine the extent to which a consolidated memory would be resistant to interference from extended practice on a different melody, practiced Melody A in the evening session, slept, and then returned in the morning to practice Melody B, before retest on Melody A (A-SLEEP-Ba).

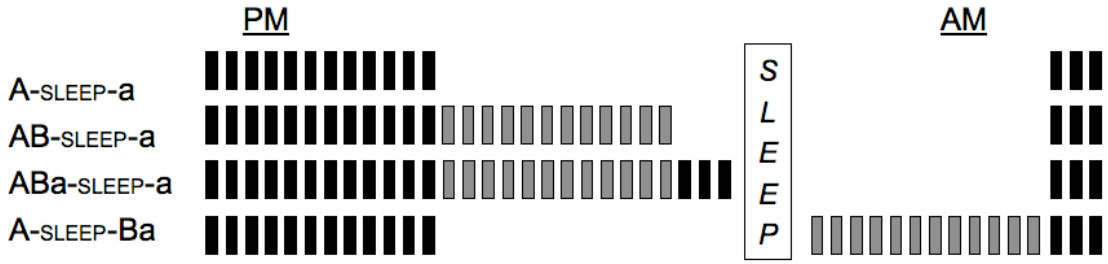

Figure 7. Design of the four experimental groups. Each rectangle represents a 30-second practice/retest block (black = Melody A, grey = Melody B), with 30 seconds rest between each block. PM and AM sessions were approximately 12 hours apart.

PROCEDURE

All subjects reported for two sessions approximately 12 hours apart, one in the evening and one on the subsequent morning. I met with subjects for sessions in the evening between 8:00-10:00PM and then again, approximately 12 hours later following overnight sleep, between 8:00-10:00AM.

The first session began with subjects' reading and signing the IRB consent form and answering questions concerning their handedness, age, music experience, piano experience, and their previous night's sleep (see Appendix B). Subjects rated their feeling of alertness using the Stanford Sleepiness Scale (Hoddes, Zarcone, Smythe, Phillips, & Dement, 1973) (see Appendix C) and reported the number of hours slept in the previous night. Prior to beginning the study, subjects had agreed to refrain from drugs, alcohol, and caffeine, substances that are known to alter cognitive function, for 12 hours prior to and during the experiment and to get a full night's sleep between evening and morning testing sessions.

After subjects completed the paperwork and questionnaire, I briefly explained the experimental procedure and oriented subjects to the computer program. The melody was displayed on the computer screen in front of them, with the fingerings indicated below the music notation (see Figure 8). Above each note was an unfilled circle. The circles illuminated one at a time in order from left to right with each keypress, regardless of whether the keypress was correct, in order to help subjects maintain their place in the sequence and remain in sync with the computer's recording of their playing.

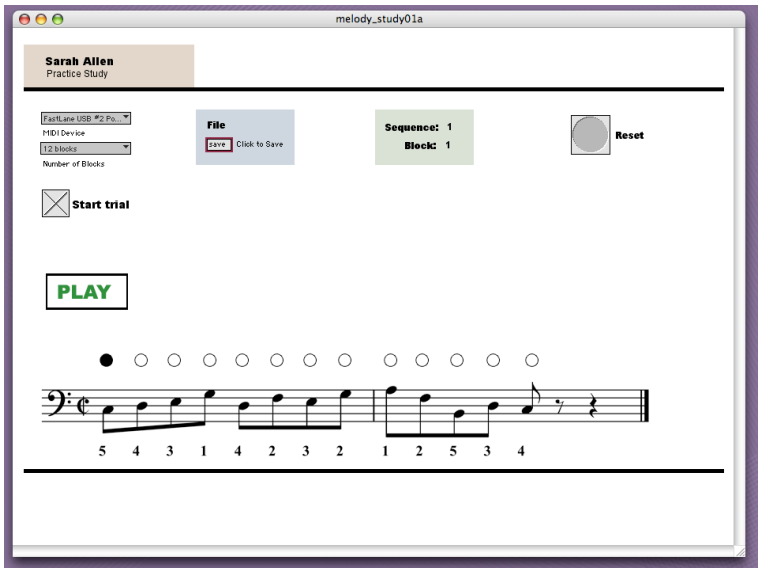

Figure 8. Image of computer screen as seen by participants during the experiment.

This protocol is common for studies using similar tasks (Duke & Davis, 2006; Kuriyama, Stickgold, & Walker, 2004; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002). The procedure required subjects play the melody repeatedly, from beginning to end, during each of 12 30-second practice blocks.

The following instructions were read aloud prior to the beginning of practice:

> You will learn a 13-note sequence of notes on this keyboard. You will play the sequence with your left hand and will use the fingerings written under the staff. Remember that '5' is your left pinky and '1' is your left thumb. Please play through the melody slowly enough to play these notes accurately with the fingerings indicated. Do you have any questions about what you see?

At this point subjects played through the melody slowly until they demonstrated the ability to play the melody with all of the correct notes and fingerings. Necessary adjustments to piano volume, headphones, and seating position were made at this time to facilitate subjects' comfort and ease of practice. Following this, I read:

> The sequence and fingering indications will be displayed continuously on the computer screen. The unfilled circles that you see above the staff correspond to each note, so that you can keep track of where you are. Each circle will illuminate after the computer has recorded its corresponding note. The circles will be illuminated regardless of whether you play the correct pitch; they are only there to help you keep track of where you are in the sequence. The computer simply counts the first 13 notes that you play, so it is important that you not start over again or try to replay a note that you might miss. Do your best to play the melody from beginning to end each time without stopping. Do not practice specific parts out of context or vary the rhythmic pattern; in other words, play it just as written. If you play a wrong note or hit an extra key at any point, try to pick up the sequence at the next note and continue on with practice without pause. Before we begin recording data, I'm going to start the program so you can play a few practice trials to orient yourself to the way it will work. Play through the sequence twice now to make sure this makes sense to you.

Subjects then played through the melody slowly twice more (now with the computer program); if subjects failed to follow the instructions (e.g., they started and stopped, repeated notes, or did not continue after an error), I repeated the verbal instructions and had them repeat the sequence until they could play it correctly. Following this, and before I began the first training block, I read:

> You will play the sequence over and over continuously for 30 seconds, followed by a brief 30-second rest period before the next practice block. You will see the word "PLAY" appear on the computer screen above the sequence. This indicates that the computer is ready to record your performance. You may then start playing when you are ready. When the 30 seconds of practice is over, you will see the word "Stop." You will do this 12 times, for a total of 12 practice blocks. Your goal is to play the sequence as quickly, accurately, and evenly as possible. Do you have any questions?

Following these instructions, I set the configurations for the computer program, and subjects began practice in their first 30-second practice block. Subjects then continued to practice the same melody for 12 30-second blocks, resting 30 seconds between blocks, for a total of 12 minutes. During the 30-second breaks, I talked with participants informally about their music background, training, major, and interests.

The computer program recorded data, beginning with the subject's first keypress, during the 30 seconds of each practice block. The words "PLAY" (in green text) or "STOP" (in red text) on the screen indicated to subjects where they were in the playing and resting sequence (as shown in Figure 8). At the conclusion of the 12th practice block of Melody A, subjects in the AB-SLEEP-a group and the ABa-SLEEP-a group began practice on a second melody, which was the retrograde form of the Melody A (shown in Figure 6). Practice on the second melody was identical to the first.

Subjects in the AB-SLEEP-a group and the ABa-SLEEP-a group began practice on Melody B approximately 30 seconds after the completion of the 12th practice block of the first melody. I instructed these subjects that practice was to continue in the same manner, and the printed music for the melody was placed in front of them. As I had done with the previous melody, I had subjects play two repetitions of this melody to demonstrate to me that they could play the notes with the correct fingerings before beginning the first practice block. The computer program was not used during practice on Melody B. I used a stopwatch to maintain the 30-second intervals precisely, and manually kept track of each of the practice blocks. Throughout all practice and retest blocks, I kept detailed notes describing any relevant events.

After learning Melody B, subjects in the AB-SLEEP-a group were dismissed. Subjects in the ABa-SLEEP-a group were then immediately retested on Melody A for three 30-second blocks alternating with 30-second rest intervals, using the Max/MSP computer program.

Subjects in the A-SLEEP-a group and the A-SLEEP-Ba group engaged in no other practice activity beyond Melody A during the training session.

At the end of their evening training sessions, all subjects were reminded to refrain from caffeine, alcohol, and drugs before the next meeting, to avoid practicing their

instrument before the next meeting, and to get a good night's sleep, and were told when to arrive the next morning for the second session.

Upon arrival for the morning session, all subjects again rated their feelings of alertness using the Stanford Sleepiness Scale and reported the number of hours slept in the previous night. They also reported any music practice or use of drugs, alcohol, or caffeine between sessions.

In the morning session, the A-SLEEP-a, the AB-SLEEP-a, and the ABa-SLEEP-a groups were retested on Melody A for 3 30-second blocks separated by 30-second rest intervals, using the Max/MSP computer program. As with the evening training sessions, we talked briefly about their musical background and interests during the 30-second rest breaks. Retests were limited to only 3 blocks in order to rule out the possibility that retest would serve as additional practice (Walker et al., 2003).

The A-SLEEP-Ba group, however, began the morning session by learning and practicing Melody B for 12 30-second blocks, in the same manner as the other groups had practiced on the previous evening. This group was then retested on Melody A for 3 30-second blocks.

Upon completion of the study, all participants signed the Payment Release Form and received $10 compensation.

DATA ANALYSIS

Data for individual trials and practice blocks were recorded using Max/MSP as tab-delineated text files, imported into Microsoft Excel, and compared across the training and retest sessions.

I measured performance in terms of the number of correct keypresses per 30-second block (CKP/B). This measure was devised in a previous study with a similar task

(Duke & Davis, 2006). The measure of CKP/B is a single measure that reflects both speed and accuracy.

The computer software tagged all note errors during participants' performances; I then visually examined every error in the individual data files to identify errors that were anomalous and unrepresentative of participants' performance accuracy (e.g., a performance getting out of sync with the computer program). Keypresses from partial sequences that were not yet completed when the 'Stop' signal was given after 30 seconds of practice were included in the CKP/B calculation.

Temporal evenness was measured in terms of the standard deviation of the inter-onset intervals between successive tones in each sequence. Uncompleted partial sequences at the end of training and retest blocks were utilized in this calculation as well.

IV. RESULTS

Research in psychology and neuroscience indicates that memories for newly-learned procedural skills continue to evolve offline in the hours following practice. In studies of unskilled learners performing simple motor tasks, these new memories show evidence of stabilization by 6 hours after practice, and show evidence of further performance enhancement following post-training sleep. It remains unclear however whether these same offline processes affect new procedural memories when skilled learners practice more complex tasks.

The purpose of this study was to investigate this topic by testing musicians who learn to perform brief melodies on a piano keyboard. I sought to determine the extent to which the post-training consolidation process is affected by learning different skills in juxtaposition. I posed the following questions:

1. When experienced musicians learn and practice a new musical task, one that includes visual, motor, and auditory components, does the memory for the task show evidence of delayed offline enhancement following overnight sleep?
2. When experienced musicians learn two, similar musical tasks in succession, does learning the second task interfere with the memory of the first task?
3. If so, is the interference effect a result of immediate disruption of the memory for the task learned first (a phenomenon termed *retroactive interference*), or is it a result of interference during post-training consolidation?

PARTICIPANT DATA

The 60 right-handed musicians (24F; *M* age = 25.20; *SD* = 5.01) who participated in the study reported an average of 7.23 (*SD* = 1.61) hours of overnight sleep during the night before training, and 6.79 (*SD* = 0.96) hours of overnight sleep during the night prior to retest. There were no significant correlations between amount of reported sleep before training and performance at the beginning of training, $r(58) = -0.006$, $p > .96$, or between amount of reported sleep before retest and performance at the beginning of retest, $r(58) = -0.04$, $p > .76$. There were also no significant correlations between the amount of reported sleep and performance gains during training, $r(58) = -.08$, $p > .54$, or gains between training and retest sessions, $r(58) = -.002$, $p > .98$. These results are consistent with those reported in similar experiments that tested simpler skills (cf. Review of Literature). No subjects reported the use of drugs or alcohol prior to or between testing sessions.

There were also no significant correlations between participants' performance and their reports of alertness, as assessed by the Stanford Sleepiness Scale (see Appendix C) prior to each training and retest session. The range of the Stanford Sleepiness Scale extends from 1 ("Wide awake") to 7 ("Sleep onset soon"). Participants reported a mean sleepiness rating of 2.65 (*SD* = 1.02) at the beginning of the training session and 2.76 (*SD* = 0.99) at retest, with no significant differences in sleepiness found between groups at the beginning of training, $F(3,56) = 0.83$, $p > .48$, or at retest, $F(3,56) = 0.54$, $p > .65$. There were no significant correlations between reported alertness at training and performance at the beginning of training, $r(58) = -0.03$, $p > .81$, or between reported alertness at retest and performance at the beginning of retest, $r(58) = 0.09$, $p > .49$. There were also no significant correlations between reported alertness and performance gains during training, $r(58) = .06$, $p > .64$, or gains between training and retest sessions, $r(58)$

= .01, $p > .93$. There was a small, nearly-significant correlation between hours of sleep before retest and reported sleepiness at retest, $r(58) = -0.23$, $p < .07$.

Below, I report the results for the four groups in the study. Each group's label describes the experimental condition. Uppercase letters (A and B) represent 12 blocks of practice on Melody A or B, respectively; lowercase letters (a and b) represent 3 blocks of retest on those melodies. For example, AB-SLEEP-a indicates that participants in this group learned both melodies and then were retested on the first sequence (a) following sleep. Statistical analyses were carried out using a two-factor, repeated measures analysis of variance (ANOVA) and two-tailed, paired-samples *t*-tests.

EXCLUDED DATA

Exploratory data analysis indicated that several participants represented outliers within their respective groups, either in terms of the final triplet of training, in terms of the retest triplet, or in terms of the gain score from training to retest. I defined outliers as scores that were either (1) more than 1.5 times the group interquartile range above the 75th percentile or (2) more than 1.5 times the group interquartile range below the 25th percentile.

Inclusion of these outliers in the data set understandably resulted in heterogeneity of variances among groups according to Levene's test. Thus, in all subsequent analyses of CKP/B, I omitted the outliers on the measures described above: two participants' scores from A-SLEEP-a, one participant's score from AB-SLEEP-a, and two participants' scores from A-SLEEP-Ba. In the analysis of evenness, I omitted the scores of one participant from A-SLEEP-a, one participant from AB-SLEEP-a, and one participant from ABa-SLEEP-a.

PERFORMANCE DATA

Performance of the primary task in this study (Melody A) was measured by 30-second practice block in terms of both correct keypresses per block (CKP/B) and temporal evenness (the block mean of inter-onset-interval standard deviations for each trial, or IOI SDs).

I compared CKP/B and IOI SD scores by first averaging the CKP/B and IOI SD block means in consecutive triplets of 3 blocks each, as depicted in Figures 9 and 10.

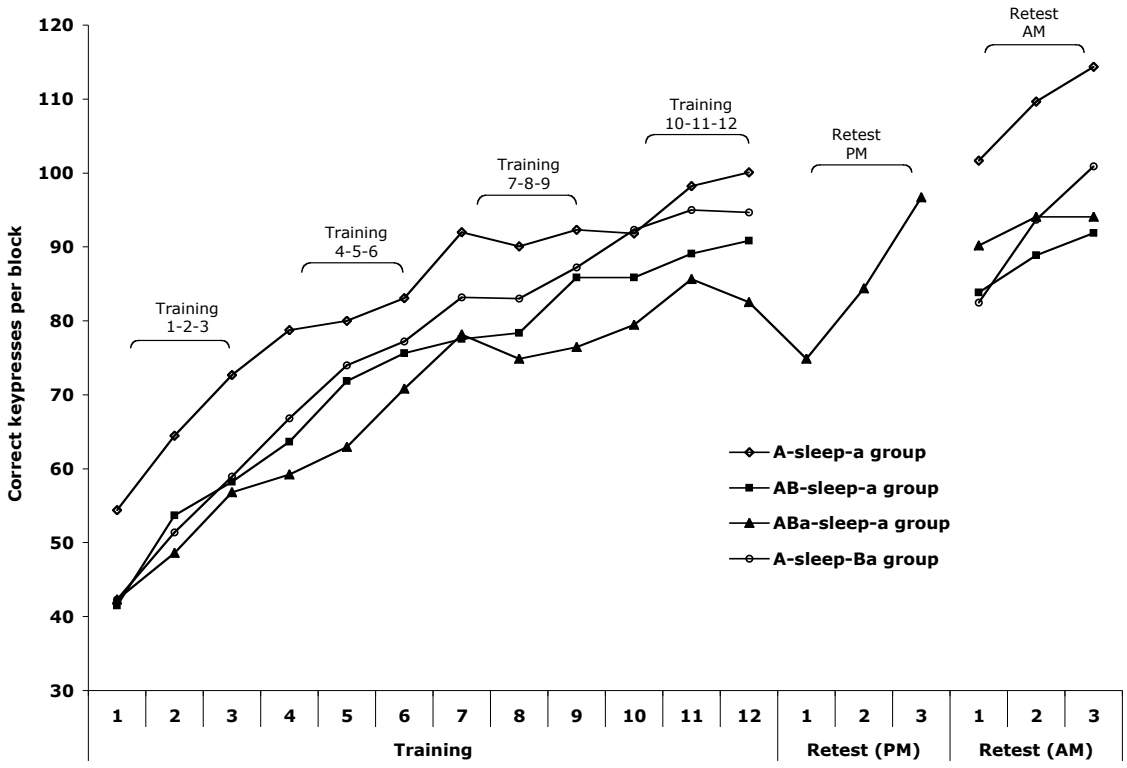

Figure 9. Group CKP/B means for all training and retest blocks.

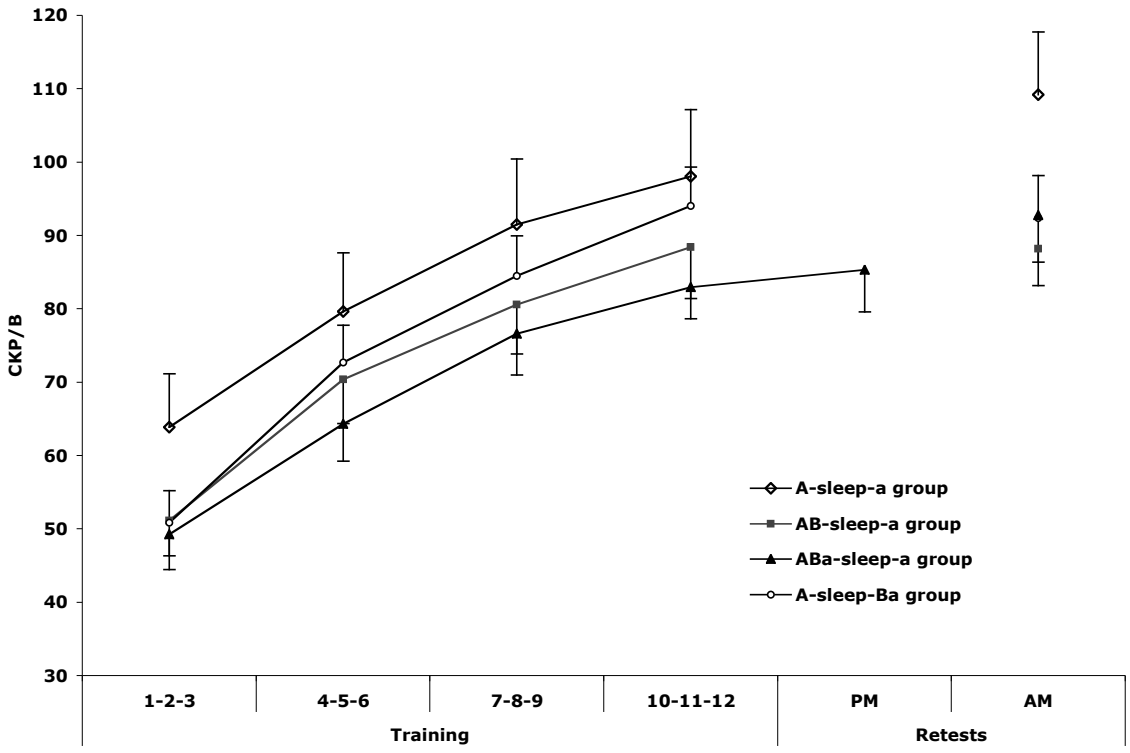

Figure 10. Group CKP/B means for training and retest block triplets. Error bars indicate ±1 SE.

I analyzed participants' performance from the end of training to retest using a two-way repeated measures analysis of variance (ANOVA): group by time point (the last triplet of training and the retest triplet). Results indicate a significant increase in CKP/B from training to retest, $F(1, 51) = 6.83$, $p = .012$; no significant difference among groups, $F(3, 51) = 1.30$, $p > .28$; and a significant interaction between group and time point, $F(3, 51) = 3.25$, $p = .029$, an indication of the overnight consolidation effects attributable to experimental conditions.

Analysis of evenness showed no significant increase between the end of training and retest, $F(1, 53) = 1.80$, $p > .18$; a significant difference among groups, $F(3, 53) =$

4.52, $p = .007$; and no significant interaction between group and time point, $F(3, 53) = 0.31$, $p > .81$.

All groups made robust gains in both CKP/B and evenness during the training session. Overall, there was a gain of 69.0% in CKP/B during training, from 53.56 CKP/B (*SE* = 2.83) in the first block triplet of training to 90.52 CKP/B (*SE* = 3.30) in the last block triplet of training. This represents an improvement in speed from a mean of 60 beats per minute (bpm) to a mean of 107 bpm.

There was also a 53.2% overall improvement in evenness during training, with changes in IOI SDs from 178.11 ms (*SE* = 17.70) in the first block triplet of training to 83.37 ms (*SE* = 6.33) in the last block of training (as shown in Figure 11). Post hoc analyses of the between-group differences (with Bonferroni adjustments for multiple comparisons) indicate that the A-SLEEP-a and AB-SLEEP-a groups performed significantly more evenly across training and retest than did participants in the ABa-SLEEP-a group, $p < .043$. The overall evenness means for the A-SLEEP-a, AB-SLEEP-a, and A-SLEEP-Ba groups were not significantly different from one another. The greater unevenness observed in the ABa-SLEEP-a group across training and retest is small (approximately 40 ms) and seems unrelated to the consolidation process under investigation.

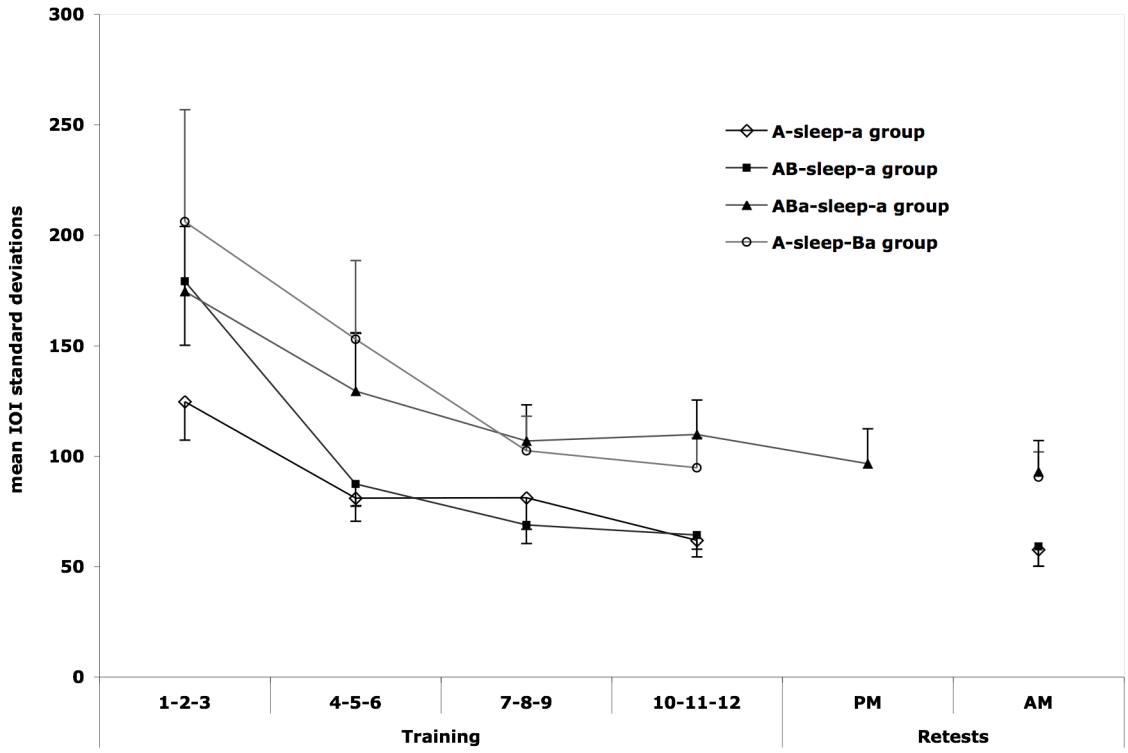

Figure 11. Group evenness means for training and retest block triplets, as measured by the mean inter-onset-interval standard deviations, or IOI SDs. Error bars indicate ±1 SE.

PERFORMANCE OF THE A-SLEEP-A GROUP

I observed evidence of delayed offline performance gains in the A-SLEEP-a group, who learned the first melody in the evening and was retested on the following morning, following overnight sleep (Figure 12). This group exhibited significant improvement in CKP/B from the end of training to retest, improving from an average of 98.04 CKP/B (*SE* = 9.09) to 109.17 CKP/B (*SE* = 8.60), $t(12) = 3.77$, $p = .003$.

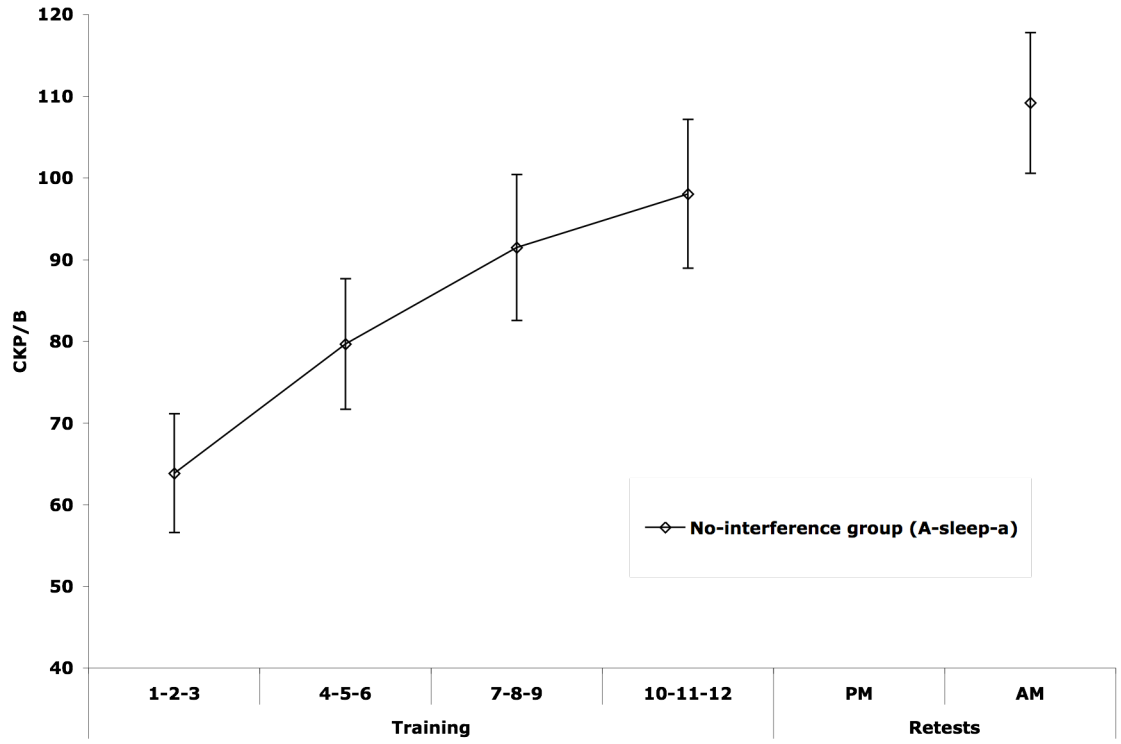

Figure 12. Mean CKP/B for the A-SLEEP-a group at training and retest. Error bars indicate ±1 SE.

This between-session improvement (+11.4%) is similar in magnitude to the improvements observed in previous research with a variety of different skills (e.g., Balas, Roitenberg, Giladi, & Karni, 2007; Dorfberger, Adi-Japha, & Karni, 2007; Duke & Davis, 2006; Walker, Brakefield, Hobson, & Stickgold, 2003). This group exhibited no overnight improvement in evenness at retest.

PERFORMANCE OF THE AB-SLEEP-A GROUP

In the AB-SLEEP-a group, who learned a second melody (Melody B) immediately after learning the target melody (Melody A), the practice of Melody B inhibited overnight

gains observed in the A-SLEEP-a group at retest following sleep (Figure 13). This group showed no overall overnight enhancement in Melody A, performing very similarly at the end of training and at retest (training = 88.4 CKP/B, *SE* = 7.00; retest = 88.2 CKP/B, *SE* = 5.02), $t(13) = 0.047$, $p = .96$.

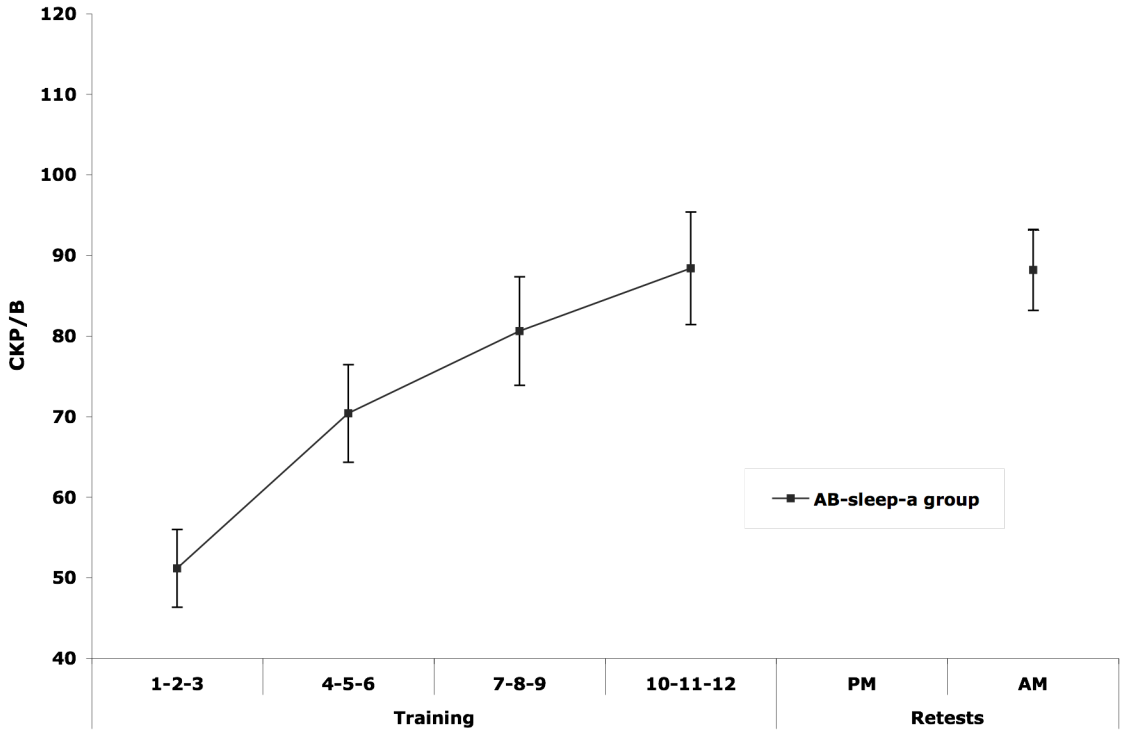

Figure 13. Mean CKP/B for the AB-SLEEP-a group at training and retest. Error bars indicate ±1 SE.

This finding is consistent with the results of previous research, which demonstrate that practice on a second, similar task can interfere with the offline processes that lead to overnight gains in a task learned first (e.g., Balas, Roitenberg, Giladi, & Karni, 2007; Dorfberger, Adi-Japha, & Karni, 2007; Duke & Davis, 2006; Walker, Brakefield, Hobson, & Stickgold, 2003). There was also no improvement in evenness in this group at retest.

PERFORMANCE OF THE ABA-SLEEP-A GROUP

The purpose of this group was to test the extent to which the interference from learning Melody B was immediate (i.e., retroactive interference) or delayed (i.e., interference during consolidation). The ABa-SLEEP-a group was retested briefly on Melody A at the end of training, prior to sleep. They showed a mean CKP/B gain of only 2.8%, from 83.0 CKP/B (*SE* = 4.32) to 85.3 CKP/B (*SE* = 5.72), when tested immediately following the learning of Melody B, prior to overnight sleep (Figure 14). However, at the morning retest session, this group exhibited a significant gain in mean CKP/B of 11.8% (from the end of training), $t(14) = 2.39$; $p = .031$. No offline gains in evenness were evident for this group at retest.

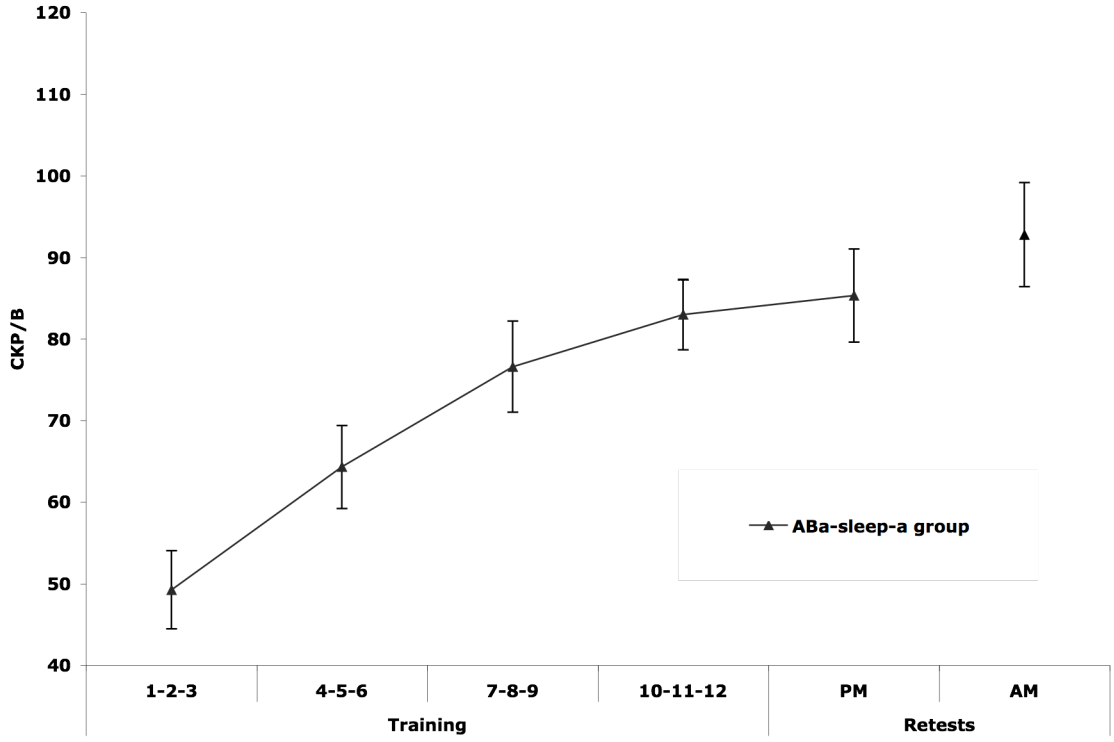

Figure 14. Mean CKP/B for the ABa-SLEEP-a group at training and retest. Error bars indicate ±1 SE.

The ABa-SLEEP-a group CKP/B improved considerably *within* the 3 individual retest blocks of Melody A immediately following training on Melody B, with CKP/B increasing 29.1% from block 1 to block 3 of retest (see "Retest PM" blocks in Figure 15).

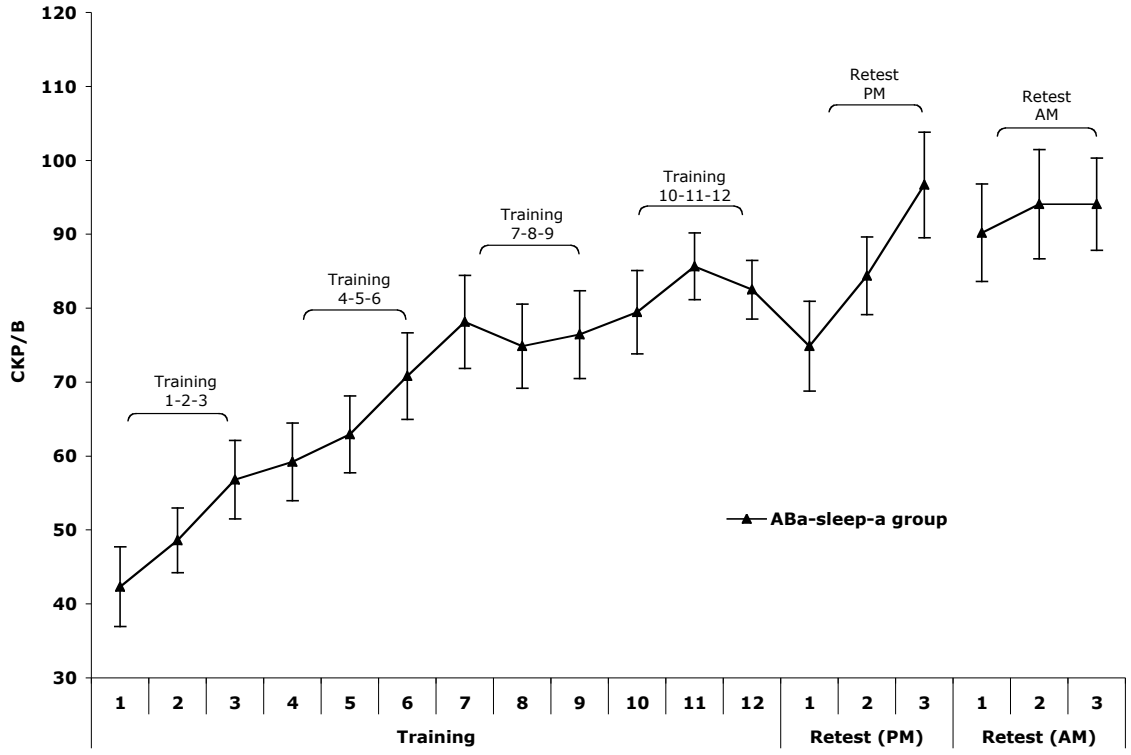

Figure 15. The ABa-SLEEP-a group CKP/B means for training and retest blocks. Error bars indicate ±1 SE.

PERFORMANCE OF THE A-SLEEP-BA GROUP

The A-SLEEP-Ba group learned Melody A in the evening training session, and then practiced Melody B for 12 blocks in the morning, prior to the brief retest on Melody A. At the end of the evening session, this group had a reached a mean of 94.00 CKP/B (*SE* =3.47), but at the morning retest session had a mean of just 92.36 CKP/B (*SE* = 4.68), a

loss of 1.75% (as shown in Figure 16). This was not a significant difference, $t(12) = 0.52$; $p > .60$. This group exhibited no overall overnight improvement in evenness.

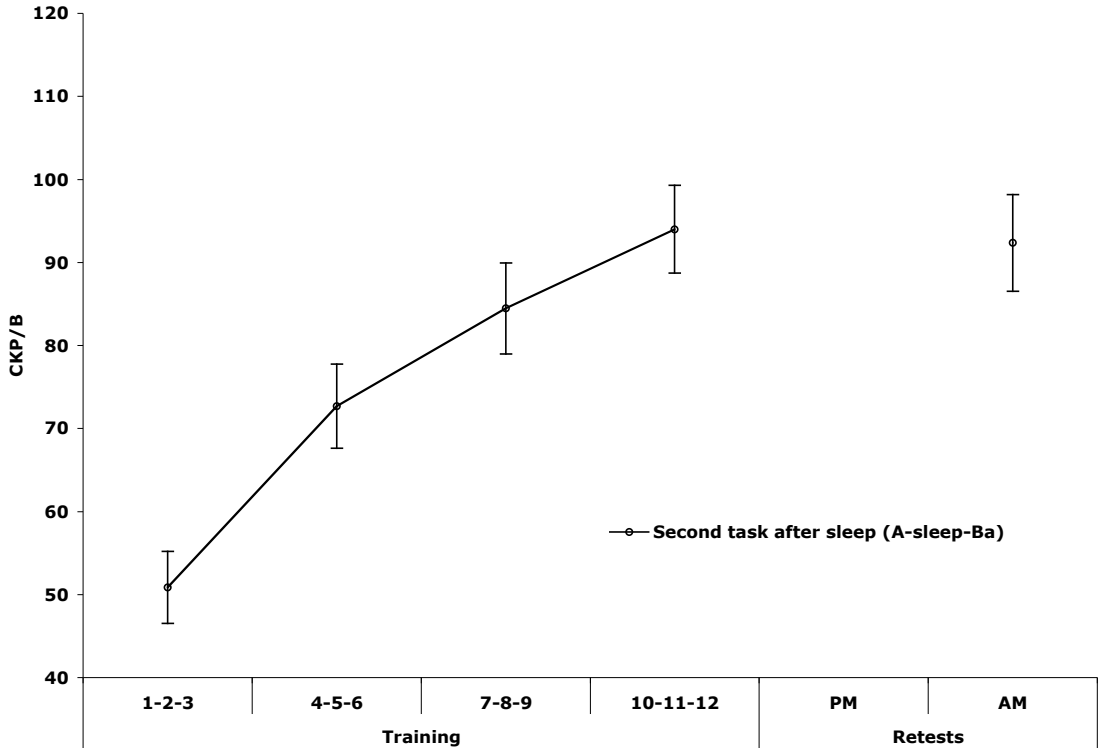

Figure 16. Performance of the A-SLEEP-Ba group at training and retest (mean CKP/B). Error bars indicate ±1 SE.

It should be noted, however, that the A-SLEEP-Ba group also improved at a very high rate (+22.4%) *within* the 3 individual blocks of the morning retest on Melody A, with mean CKP/B increasing from 82.46 CKP/B (*SE* = 5.68) to 100.92 CKP/B (*SE* = 5.67) (see Figure 17). Recall that there was no break between practice on Melody B and retest of Melody A for this group; the morning retest condition for this group is thus different than the retests of three other groups. It is possible that diminished performance of this group at the beginning of retest reflects a more immediate interference from having just practiced Melody B. If this is the case, the effects of this interference did not

appear to be long-lasting for this group, however, in that by the second block of retest participants' performance returned to the level reached by the end of training on Melody A (M = 89.86 CKP/B, *SE* = 5.84), and then continued to improve until the third block of retest.

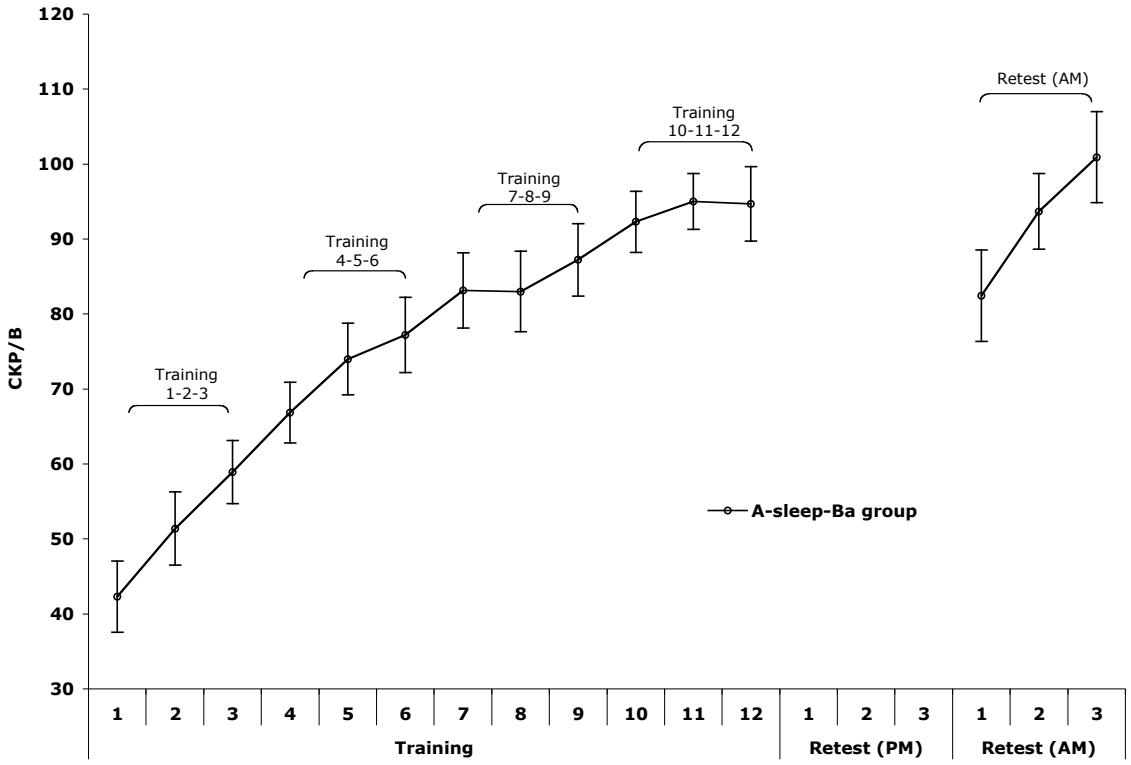

Figure 17. The A-SLEEP-Ba group CKP/B means for training and retest blocks. Error bars indicate ±1 SE.

COMPARISON OF THE A-SLEEP-A AND AB-SLEEP-A GROUPS

I compared performance of the A-SLEEP-a group and the AB-SLEEP-a group (as shown in Figure 18) to determine if learning a second, similar task interfered with the memory of a first task in musicians. As stated previously, the AB-SLEEP-a group did not exhibit overnight gains on the performance of Melody A, whereas the A-SLEEP-a group

exhibited significant gains following post-training sleep, $t(12) = 3.77$, $p = .003$. Thus, with the musical task used in this study, practice on Melody B interfered with the offline gains that would otherwise have occurred during sleep, as seen in the A-SLEEP-a group.

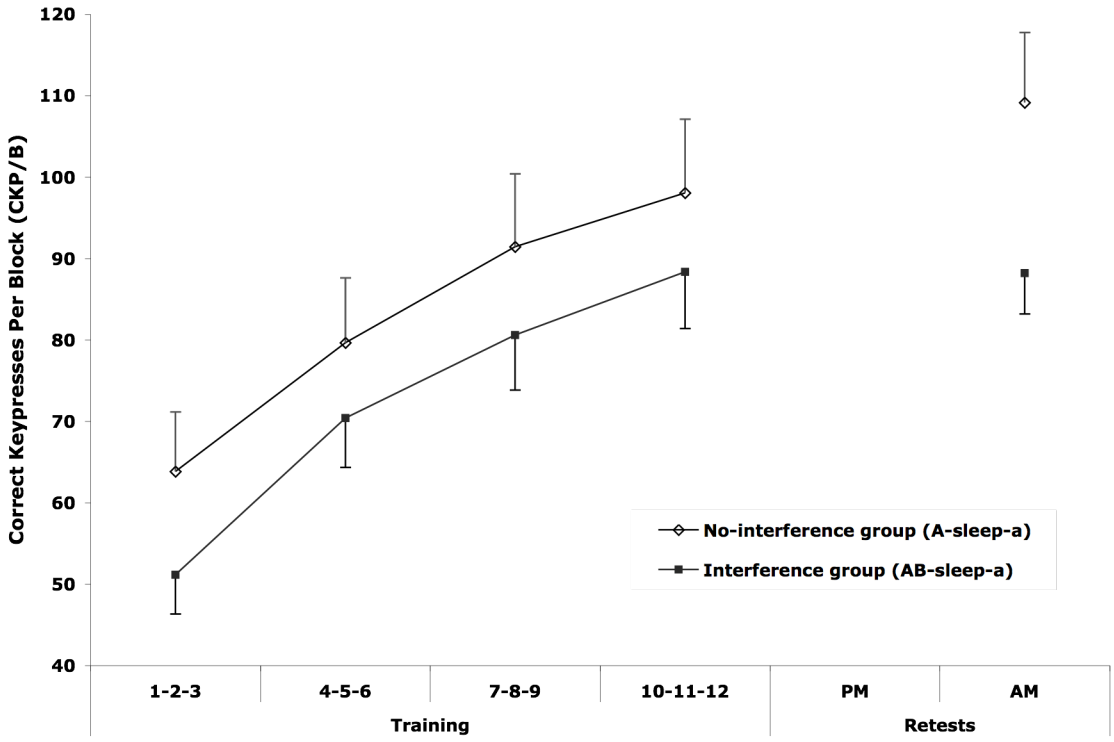

Figure 18. Performance of the A-SLEEP-a group and the AB-SLEEP-a group at training and retest (mean CKP/B).

COMPARISON OF THE AB-SLEEP-A AND ABA-SLEEP-A GROUPS

Although the AB-SLEEP-a and ABa-SLEEP-a groups both learned melodies A and B in the evening session, the groups did not perform alike at retest on Melody A following sleep (as shown in Figure 20). This is perhaps the most interesting finding in the study. Recall that the only difference between these groups was the additional, brief recall of Melody A by the ABa-SLEEP-a group at the end of the evening session.

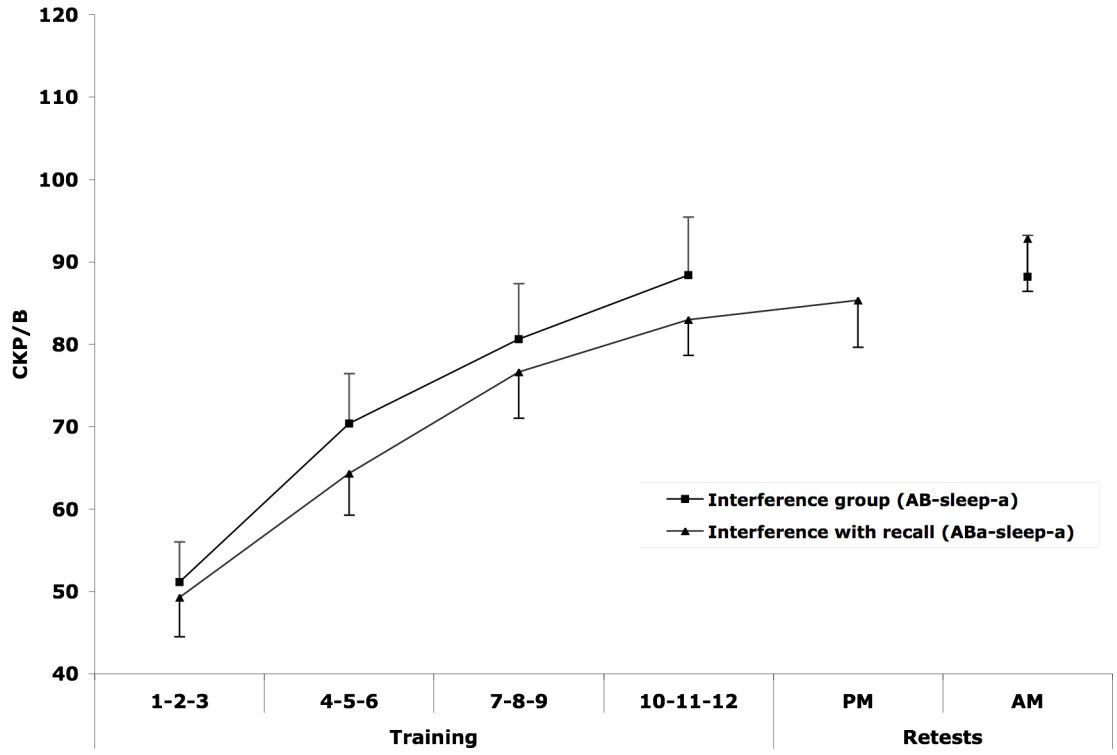

Figure 20. Performance of the AB-SLEEP-a group and the ABa-SLEEP-a group at training and retest (mean CKP/B).

Remember that the ABa-SLEEP-a group exhibited virtually no gains in CKP/B (2.8%) at retest at the end of the evening training session. This group's subsequent improvement following sleep seems to show that briefly recalling Melody A at the end of the training session led to overnight enhancement of Melody A, and perhaps served as a trigger for offline consolidation processes to begin for this skill memory. Interestingly, the difference between the mean CKP/B for this group at the end of training (83.0 CKP/B) and at the next morning's retest (92.8 CKP/B), an improvement of 11.8%, is quite similar to the overnight improvement observed in the A-SLEEP-a group (+11.4%), the group that learned only one melody (see Figure 21).

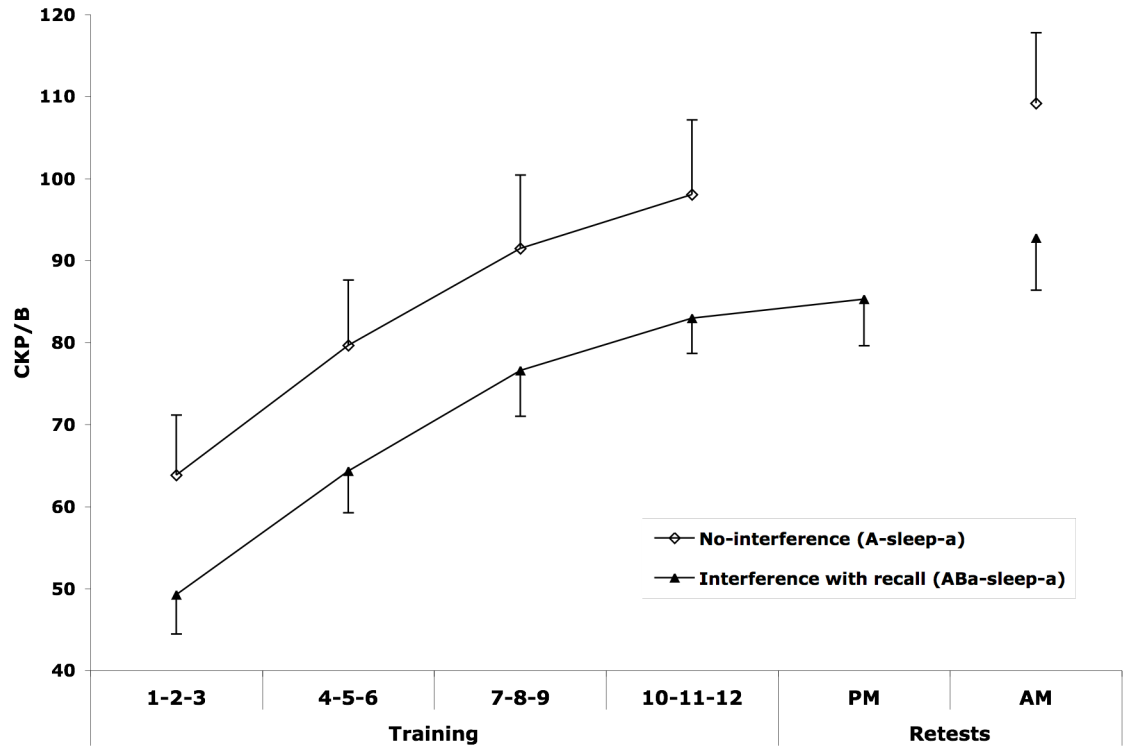

Figure 23. Performance of the A-SLEEP-a group and the ABa-SLEEP-a group at training and retest (mean CKP/B).

COMPARISON OF THE ABA-SLEEP-A AND A-SLEEP-BA GROUPS

Recall that both the ABa-SLEEP-a and the A-SLEEP-Ba groups were retested on Melody A *immediately* following 12 blocks of practice on Melody B. At this retest (which occurred in the evening for the ABa-SLEEP-a group and in the morning for the A-SLEEP-Ba group), neither group exhibited performance gains, and actually performed worse in the first retest block than at the end of the previous training. However, both groups made robust gains in mean CKP/B *within* the three blocks of this retest, with the ABa-SLEEP-a group exhibiting a 29.1% gain and the A-SLEEP-Ba group exhibiting a 22.4% gain. This performance indicates that the training on Melody B, immediately preceding the retest on Melody A, had an immediate effect upon the retest performance

of Melody A for these groups. However, the subsequently high rates of improvement in these groups *within* retest seems to reveal that this interference effect was not long-lasting.

SUMMARY OF RESULTS

In this study, I found that experienced musicians who learned and practiced a piano melody showed evidence of overnight offline gains in performance speed and accuracy (as measured in CKP/B). Practice on a second, similar melody seemed to block these overnight offline gains, indicating that the overnight consolidation of new skill memories is susceptible to interference from practice on similar tasks. Most importantly, I found in this study that the brief recall of the first melody prior to sleep (following practice on a second melody) resulted in an overnight enhancement for the first melody that was not observed in the group without this recall (AB-SLEEP-a.

V. DISCUSSION

Musicians spend countless hours learning and refining performance skills, but much remains unknown about the neural correlates of this complex and multi-sensory activity. The present study is one of the first to systematically examine procedural memory consolidation, specifically the evolution of consolidation-based stabilization and consolidation-based enhancement, in musicians learning musical tasks. Below I discuss the new results found in this study regarding skilled learners practicing complex tasks and I describe the consistencies and inconsistencies between the results of the present study and the findings reported in the extant literature.

In this study, I sought to determine whether musical tasks learned by experienced musicians show evidence of delayed offline gains following practice. All participants in the experiment practiced either one or two 13-note melodies with their nondominant hands in an evening training session and were retested the next morning, following overnight sleep.

EFFECTS OF SLEEP AND INTERFERENCE ON TEMPORAL EVENNESS

No groups showed offline improvement in evenness at retest following sleep, which is consistent with the results of previous research in which skilled learners learned a similar task (Simmons & Duke, 2006). Simmons and Duke found that significant offline gains in evenness were not observed until 24 hours after training. These findings may indicate that the consolidation processes affecting this aspect of musicians' performance extends over a longer time period than do the processes that result in

enhancements of CKP/B. The evenness of movements is not typically assessed in tests of motor sequence learning and consolidation. In music, of course, the evenness of successive tones is a hallmark of skillful playing. Although Simmons and Duke found that temporal evenness improved only after intervals of 24 hours, theirs is the only experiment to assess this variable in relation to offline consolidation effects. Thus it seemed important to include this variable in the current investigation, the null result notwithstanding.

The remainder of this discussion considers the changes that occurred in learners' accuracy and speed, expressed as CKP/B.

EFFECTS OF SLEEP AND INTERFERENCE ON SPEED AND ACCURACY IN A MUSICAL TASK

The musicians who learned one melody in the evening training session and returned for a brief retest of the melody following overnight sleep (A-SLEEP-a) clearly demonstrated overnight enhancement on this task, with a 11.4% higher mean CKP/B at retest than at the end of training. These results indicate that a new skill memory of this type and complexity exhibits observable behavioral benefits from post-training sleep.

Many researchers have reported similar offline gains in sequence-learning tasks (Balas, Roitenberg, Giladi, & Karni, 2007; Dorfberger, Adi-Japha, & Karni, 2007; Duke & Davis, 2006; Kuriyama, Stickgold, & Walker, 2004; Simmons & Duke, 2006; Walker et al., 2003). For example, in experiments that used 5- to 9-element keypress tasks without auditory feedback, Kuriyama et al. (2004) found a 20.2% improvement in speed on a 9-element keypress sequence following sleep; Dorfberger et al. (2007) found a gain of 33% in speed following sleep; and Fischer et al. (2002) observed a gain of 33.5% in the number of correct sequences per block following sleep. Measuring the number of

correct keypresses per block (as in the present study), Duke and Davis (2006) reported a gain of 16.2% CKP/B following a night of sleep.

To date, only Simmons and Duke (2006) have reported sleep-based enhancements in a musical task. The musicians who participated in their study performed with significantly fewer errors following sleep, though they showed no improvements in speed. It is important to note that all of the experiments cited above used somewhat different dependent measures, and this fact must be considered carefully when comparing the relative magnitudes of overnight enhancements attributed to sleep-based consolidation.

Researchers have postulated that offline gains are a direct result of the unique neurophysical processes involved in sleep, during which new neural pathways are often strengthened and networks associated with new memories are reorganized, absent active task practice. The cycling of sleep stages, a result of thousands of years of evolution, regulates the chemical and neurophysical processes necessary for these neurochemical and neurophysical changes to take place.

It is also possible, especially with skilled learners like those who participated in this study, that time away from task practice, particularly time during sleep, affords the brain an opportunity to connect and integrate new skill memories with existing networks of similar and related memories. Performance enhancements could be partially a result of the brain's ability to draw upon already automated, well-learned skills in the performance of a new skill. This ability would be especially useful with a complex, multi-faceted skill like piano playing, which is made up of many smaller, simpler motor components. The brain's ability to recruit existing neural circuitry to facilitate performance and recall of novel tasks could aid in efficiency; time after practice, offline, might then be necessary to

then physically organize this newly acquired information and to update existing neural networks.

Of course, the evolution of offline gains following practice has implications for music practice. Although musicians occasionally report that a difficult passage encountered during a given practice session often feels easier days later, without any further practice, there has been little systematic support for the idea that the brain refines new skill memories and integrates them into existing memories offline. This research provides interesting insight into the way music is learned, refined, stored, and recalled, though it is still much too early to formulate reliable prescriptions for music learning and practice based on the results so far obtained.

EFFECTS OF LEARNING A *SECOND* MUSICAL TASK PRIOR TO SLEEP

In order to examine the susceptibility of a new musical task to interference by a second, similar task, I had one group of participants learn two melodies in close juxtaposition during the evening training session. Following sleep, these subjects were retested briefly on the melody learned first (AB-SLEEP-a) and showed no offline performance gains at the morning retest. At the end of the evening training session, the mean CKP/B for participants in this group was 88.3 CKP/B, and at retest their mean was 88.2 (-0.21%). Clearly, no boost in performance was seen for this group following overnight sleep. This is in contrast to the A-SLEEP-a group, who learned only one melody and showed an 11.4% gain in CKP/B.

From this comparison, it seems as though learning the second melody (Melody B) for the AB-SLEEP-a group effectively blocked any subsequent offline gains that would have been expected in the retest of Melody A. These results are consistent with the findings reported in a growing number of studies examining the relative stability of new

skill memories following practice. It is clear that learning a second task at training diminishes the effects of overnight consolidation on the first task, though the nature and extent of those effects vary among experiments and tasks. Walker et al. (2003) was the first to examine this phenomenon using a sequential keypress task, demonstrating that learning two similar tasks during practice could interfere with the consolidation of the task learned first. In their study, subjects' error rates on a single keypress task decreased by an average of 35% following post-training sleep, but this improvement was not observed when subjects learned two sequences in juxtaposition. (Walker et al. found significant improvements in speed for both sequences when two were learned in the same session.)

Dorfberger et al. (2007) reported that learning two similar keypress sequences, even if the practice sessions for the two sequences were separated by two hours, eliminated any overnight gains in the first sequence that would have been observed without learning the second sequence (as measured in this study by the number of correct sequences per 30-second block). Duke and Davis (2006) reported that learners who practiced two different keypress sequences in a single training session showed improvements in CKP/B for both sequences, although the sequence learned second showed greater improvement than the sequence learned first (with a 27.9% higher CKP/B rate, as compared to an 18.2% improvement for the first task). Furthermore, Balas et al. (2007), using a 5-element sequential keypress task, found that even practicing an *unrelated*, but familiar, complex task (in this case, a handwriting task) immediately following training interfered with subsequent consolidation of the task learned first.

It could be proposed that participants in AB-SLEEP-a simply had more new information to "remember"—two tasks, instead of one task as was the case with A-SLEEP-

a. However, this cannot be the case, as the ABa-SLEEP-a group, which learned a second task as well, showed overnight improvements on the first task.

Researchers have proposed that similar tasks learned in close temporal proximity might compete for the same neural resources required for consolidation following practice. Of course, since we encounter so many new stimuli in a day, the brain must selectively consolidate those memories that are the most meaningful, important, and potentially beneficial. It seems reasonable, then, that the brain, faced with multiple new skill memories and given the constraints of processing capability, must in a sense choose which memories are most important to retain. The variables that govern the prioritization of procedural memory consolidation are not fully understood, but recent research is beginning to illuminate some of the processes involved in memory encoding, storage, and integration that occur during and following practice.

It has been shown that music skills show evidence of sleep-based enhancements attributable to consolidation (Simmons & Duke, 2006), but prior to the current study, the potential for multiple musical tasks to interfere with consolidation was unknown. Of course, musicians typically practice multiple skills in a single practice session, and the results of the present study indicate that new skill memories are susceptible to interference following practice, such that practice on similar tasks in a single training session may interfere with subsequent consolidation-based enhancement of the task learned first.

EFFECTS OF BRIEF RECALL ON A NEW SKILL MEMORY PRIOR TO SLEEP

The results obtained from the ABa-SLEEP-a group are interesting for two reasons. First, they demonstrate that learning a second melody prior to sleep did not immediately interfere with the memory of the melody learned first, as indicated by the Melody A

retest at the end of the evening session. Second, they demonstrate that recalling Melody A in the evening, after having learned Melody B, resulted in consolidation-based enhancements in Melody A overnight, enhancements that were not observed when Melody A was not recalled at the end of the evening session (AB-SLEEP-a). In other words, the recall of Melody A in this experiment may have triggered overnight consolidation-based enhancement that might otherwise have been blocked by practice on Melody B, as was observed in the AB-SLEEP-a group.

Recall that the ABa-SLEEP-a participants learned both melodies in succession during the evening session and were briefly retested on Melody A at the end of the session. Their performance at the evening retest was similar to their performance at the end of training (+2.8%), but participants in this group had a significantly higher mean CKP/B in the morning retest session, following sleep (+11.8% from the end of training). The only distinction between this group and the AB-SLEEP-a group was the additional brief recall of Melody A at the end of the evening session. However, morning retest results reveal that the ABa-SLEEP-a group showed significant gains in CKP/B at the morning retest session, while the AB-SLEEP-a group made no significant overnight improvements. It could be proposed that the ABa-SLEEP-a group simply had more opportunity to practice Melody A; however, the retest in this study was intentionally limited to only 3 blocks (a total of only 1.5 minutes), as to not constitute further task practice. Previous studies have determined that in this type of task, 3 blocks is typically insufficient to provide further learning (e.g., Walker et al., 2003).

Walker and his colleagues used a similar procedure in their study of consolidation (2003), in which subjects learned two sequences in a single training session and were then immediately retested on both. Learners showed no change in performance from the end of training to retest on either sequence. Unlike the present study, though, Walker et

al. did not retest this group again after sleep. This group in Walker's study was designed as a control to demonstrate that the interference effects of learning the second sequence did not *immediately* affect the memory of the first sequence in any way, but rather affected the overnight enhancement of the first sequence (as Walker et al. observed in a different experimental group). No study to date has examined the effect on overnight consolidation of a brief recall of a learned task (e.g., Melody A, in the current study) after having learned a second, similar task.

EFFECTS OF LEARNING A SECOND MUSICAL TASK *FOLLOWING* SLEEP

The A-SLEEP-Ba group in this study learned Melody A in the evening training session, and then returned after overnight sleep to learn Melody B before being retested on Melody A. The results of this group were unanticipated; I had hypothesized that the A-SLEEP-Ba group would perform similarly at retest to the A-SLEEP-a group. That is, that sleep (following practice on Melody A) would allow for consolidation-based stabilization and enhancement processes to proceed uninterrupted overnight, and that Melody A would thus exhibit offline gains in performance at retest in the morning, unaffected by training on Melody B.

In fact, the results from the A-SLEEP-Ba group indicate that training on Melody B in the morning, prior to retest on Melody A, obscured offline gains that might otherwise have been observed between training and retest on Melody A (as was seen in the A-SLEEP-a group, for example). It seems likely that the 12 blocks of practice on Melody B made it difficult for participants in this group to reorient to the performance requirements of Melody A immediately following. It is notable that the improvements block to block within the morning retest for Melody A are the greatest improvements of any retest in the experiment. From block 1 to block 3, this group makes very large improvements in

CKP/B (+22.4%). In fact, the group's performance on the first retest block is actually worse than at the end of training, but performance improves rapidly, recovering to training levels by block 2, and improving greatly by block 3.

Such a "disorientation" has not been discussed in existing memory consolidation literature. Perhaps its presence in the current investigation has to do with the complexity and multisensory nature of the tasks, involving both auditory feedback and the accompanying musical meaning that for musicians is inherent in a musical phrase. The 13-note melody used in this study required subjects to read and process written musical notation while performing a melody that required each finger to play multiple pitches. In other words, completing the sequence did not simply require that subjects push down the correct fingers in the correct order, but also that they *find* the correct key for each finger to press. This aspect certainly added complexity to this skill, both in terms of the motor skill component as well as the cognitive demands involved. In comparison, the two tasks typically used in other motor consolidation studies (e.g., practicing 5-4-2-1-5 or 2-3-4-1-2 on a numeric keypad) tend to be simpler both in terms of motoric and cognitive demands.

The auditory feedback present in music also added an important dimension to the motor tasks studied in this experiment. To the skilled musicians who participated, each of the two musical tasks comprised a recognizable melodic phrase, which likely added another element of complexity not present in other studies involving two simpler tasks (without additional feedback processing requirements). This distinction may have also played a role in the need for participants in this group to reorient themselves to practice on the second task.

OTHER CONSIDERATIONS

There are several aspects of this study that warrant further research. However, it should be noted that even despite these observations, I report significant differences in this study that had not previously been found in musicians regarding the role of overnight sleep, second task practice, and brief recall on the consolidation of musical tasks.

First, it should be noted that the practice utilized in the present study was not fully representative of a real musical context; musicians usually do not practice with the simple goal of playing "as quickly and accurately as possible"—typically many notes in music performance are played with inflection and with attention to dynamics and articulation. In addition, the constraints of the computer program did not allow subjects to correct errors as they normally might, but instead required them to perform the melodies from beginning to end every time. This type of practice was most likely different than the type of practice to which the musicians in this study were accustomed.

In addition, both the visual and auditory feedback from the program may have encouraged participants to favor accuracy over speed in their performance of the sequence, as performing the melody inaccurately caused performance to fall out of sync with the computer program. Of course, it is also likely that participants might have favored accuracy over speed because most have had years of musical training by teachers insisting on correct notes, and because with such a recognizable melody, avoidance of error is naturally a prominent goal. Despite these considerations, however, the participants in this study still exhibited the effects of overnight consolidation in CKP/B on these melodies.

Although all participants performed with the same computer program, many participants chose to watch their hands while performing, glancing at the screen from time to time to ensure that they were in sync. Some chose to look at the computer screen

the entire time, relying on their sense of touch to find and play the correct notes on the keyboard. I intentionally gave no specific instructions in this regard, as my interest lay in their ability to perform the sequence, and thus I allowed them to choose whichever method enabled them to best perform the sequence.

CONCLUSION

This study has much to contribute to the existing literature on motor memory consolidation. First, I examined the process of skill acquisition and consolidation in the context of experienced learners. Although researchers have more recently begun to examine differences in the learning process attributed to differences in task familiarity (Balas, Roitenberg, Giladi, & Karni, 2007) and differences in age (Dorfberger, Adi-Japha, & Karni, 2007), little is yet known about motor skill acquisition and consolidation in skilled learners.

Second, this study examines the process of skill acquisition and consolidation for complex tasks. The task in this study was challenging and complicated for learners, not only because of the long sequence length (13 keypresses rather than the 5 keypresses often used in other studies), but also because of the added auditory processing demands. Subjects were trying not only to read the music notation and fingerings on the screen in bass clef (as using finger numbers alone was not sufficient—each finger was used for more than one pitch), but also to respond to the sounds they were hearing (e.g., wrong notes, unevenness, hesitations). This offers insight not only into motor skill learning with musicians and musical tasks in particular, but also into skill learning in general that involves performing more complex tasks.

The present study has also replicated the findings of Simmons and Duke (2006) and Simmons (2007), which show consolidation-based enhancement in musicians who

practiced a novel motor skill. The present study also adds to this existing research by introducing additional task practice on a second task, contributing to our understanding of the offline processes that occur during wake following learning.

Though it would certainly be tempting at this time to offer prescriptions for musical practice and pedagogy, such generalizations are unwarranted at this time and will require much additional, systematic research. The present findings do, however, provide insight into the complex and multi-sensory activity that comprises music skill learning. Furthermore, although further research is needed to more fully understand the neural processes underlying the behavioral findings in the present study, this research study begins to illuminate the process of motor learning in the context of music performance.

Appendix A

Allen – dissertation study

Participant Questionnaire Form

TRAINING SESSION (PM):

Name: _____ Subject #: _____ Group: _____

How do you feel right now? *(e.g., energetic, ill, upset)* _____ Sleep # _____

Which is your dominant hand? R L Gender: M F

Are you a music major? Y N Age: _____

Principal instrument: _____ Years of study: _____

What other instruments have you studied? _____

For how long? _____

Have you ever taken piano lessons? Y N How long? _____ At what age? ____

How many semesters of class piano have you completed? _____

How much sleep did you get last night? _____ hours *Well / Restlessly*

Is that a typical amount of sleep for you? Y N

Have you had any caffeine, alcohol, or drugs in the last 12 hours? Y N

If yes, how much of what? _____

Observations:

RETEST SESSION (AM):

How do you feel right now? *(e.g., energetic, ill, upset)* _____ Sleep # _____

Have you had any caffeine, alcohol, or drugs since we met last time? Y N

If yes, how much of what? _____

Did you play a music instrument yesterday after we met? Y N

If so, which instrument and for how long? _____

Did you play a music instrument before our meeting today? Y N

If so, which instrument and for how long? _____

How much sleep did you get last night? _____ hours *Well / Restlessly*

Observations:

Appendix B

CONSENT FORM

The Effects of Memory Consolidation and Interfering Tasks on Musicians' Performance of a Motor Sequence

IRB PROTOCOL # 2007-04-0005
Conducted by: Sarah E. Allen
Center for Music Learning, School of Music, The University of Texas at Austin
Telephone: (512) 471-2466
Email: sarahallen@mail.utexas.edu

You are being asked to participate in a research study. This form provides you with information about the study. The person in charge of this research will also describe this study to you and answer all of your questions. Please read the information below and ask questions about anything you do not understand before deciding whether or not to take part. Your participation is entirely voluntary and you can refuse to participate without penalty or loss of benefits to which you are otherwise entitled. You can stop your participation at any time and your refusal will not impact current or future relationships with UT Austin or participating sites. To do so simply tell the researcher you wish to stop participation.

The purpose of this study is to examine the effects of memory consolidation and interfering tasks on memory of a motor sequence in musicians.

If you agree to be in this study, we will ask you to do the following things:

* Practice a simple sequence on a digital piano during a training session conducted in the evening.
* Practice a simple sequence on a digital piano during a retest session conducted the following morning.
* Abstain from consuming caffeine, alcohol, and drugs 12 hrs prior to and during this study.

Total estimated time to participate in study is 1 hour.

Risks and Benefits: The risk associated with this study is no greater than everyday life. Other than monetary compensation, there are no benefits for participation in this study.

Confidentiality:

* Training and retest sessions will be taped. Data will be coded so that no personally identifying information is present.
* The records of this study will be stored securely and kept confidential. Authorized persons from The University of Texas at Austin and members of the Institutional Review Board have the legal right to review your research records and will protect the confidentiality of those records to the extent permitted by law. All publications will exclude any information that will make it possible to identify you as a subject.
* Records will be reviewed only for research purposes by the investigator and her associates, and will be retained for possible future analysis.

Compensation: You will be compensated in the amount of $10.00 for your participation.

The **records** of this study will be stored securely and kept private. Authorized persons from The University of Texas at Austin, members of the Institutional Review Board, and (study sponsors, if any) have the legal right to review your research records and will protect the **confidentiality** of those records to the extent permitted by law. All publications will exclude any information that will make it possible to identify you as a subject.

Contacts and Questions:
If you have any questions about the study please ask now. If you have questions later, want additional information, or wish to withdraw your participation call the researchers conducting the study. Their names, phone numbers, and e-mail addresses are at the top of this page. If you have questions about your rights as a research participant, complaints, concerns, or questions about the research please contact Jody Jensen, Ph.D., Chair, The University of Texas at Austin Institutional Review Board for the Protection of Human Subjects at (512) 232-2685 or the Office of Research Support and Compliance at (512) 471-8871 or email: orsc@uts.cc.utexas.edu.

You will be given a copy of this information to keep for your records.

Statement of Consent:

I have read the above information and have sufficient information to make a decision about participating in this study. I consent to participate in the study.

Signature:_____ Date: _____

Signature of Investigator:_____ Date: _____

Appendix C

Stanford Sleepiness Scale

This is a quick way to assess how alert you are feeling. You would choose a rating of a one at the most alert time during your day. Please choose which rating fits your state of alertness right now.

Degree of Sleepiness	**Rating**
Feeling active, vital, alert, or wide awake	1
Functioning at high levels, but not at peak; able to concentrate	2
Awake, but relaxed; responsive but not fully alert	3
Somewhat foggy, let down	4
Foggy; losing interest in remaining awake; slowed down	5
Sleepy, woozy, fighting sleep; prefer to lie down	6
No longer fighting sleep, sleep onset soon; having dream-like thoughts	7
Asleep	X

References

Abel, T., & Lattal, K. M. (2001). Molecular mechanisms of memory acquisition, consolidation, and retrieval. *Current Opinion in Neurobiology, 11*, 180-187.

Allen, S., & Duke, R. (2007). *Effects of interference task familiarity and complexity on motor skill consolidation*. Paper presented at the Texas Music Educators Association, San Antonio, Texas.

Ashe, J., Lungu, O., Basford, A., & Lu, X. (2006). Cortical control of motor sequences. *Current Opinion in Neurobiology, 16*, 213-222.

Atienza, M., Cantero, J. L., & Dominguez-Marin, E. (2002). The time course of neural changes underlying auditory perceptual learning. *Learning & Memory, 9*(3), 138-150.

Atienza, M., Cantero, J. L., & Stickgold, R. (2004). Posttraining sleep enhances automaticity in perceptual discrimination. *Journal of Cognitive Neuroscience, 16*(1), 53-64.

Balas, M., Netser, S., Giladi, N., & Karni, A. (2007). Interference to consolidation phase gains in learning a novel movement sequence by handwriting: dependence on laterality and the level of experience with the written sequence. *Experimental Brain Research*.

Balas, M., Roitenberg, N., Giladi, N., & Karni, A. (2007). When practice does not make perfect: well-practiced handwriting interferes with the consolidation phase gains in learning a movement sequence. *Experimental Brain Research, 178*(4), 499-508.

Baraduc, P., Lang, N., Rothwell, J., & Wolpert, D. (2004). Consolidation of dynamic motor learning is not disrupted by rTMS of primary motor cortex. *Current Biology, 14*, 252-256.

Born, J., & Wagner, U. (2004). Awareness in memory: being explicit about the role of sleep. *Trends in Cognitive Sciences, 8*(6), 242-244.

Brashers-Krug, T., Shadmehr, R., & Bizzi, E. (1996). Consolidation in human motor memory. *Nature, 382*(6588), 252-255.

Brown, R. M., & Robertson, E. M. (2007). Inducing motor skill improvements with a declarative task. *Nature Neuroscience, 10*(2), 148.

Butefisch, C., Davis, B., Wise, S., Sawaki, L., Kopylev, L., Classen, J., et al. (2004). Mechanisms of use-dependent plasticity in the human motor cortex. *Proceedings of the National Academy of Sciences, 97*(7), 3661-3665.

Caithness, G., Osu, R., Bays, P., Chase, H., Klassen, J., Kawato, M., et al. (2004). Failure to consolidate the consolidation theory of learning for sensorimotor adaptation tasks. *Journal of Neuroscience, 24*(40), 8662-8671.

Chaffin, R., Imreh, G., & Crawford, M. (2002). *Practicing Perfection: Memory and Piano Performance*: Lawrence Erlbaum Associates.

Classen, J., Liepert, J., Wise, S. P., Hallett, M., & Cohen, L. G. (1998). Rapid plasticity of human cortical movement representation induced by practice. *J ournal of Neurophysiology, 79*(2), 1117-1123.

Coffman, D. D. (1990). Effects of mental practice, physical practice, and knowledge of results on piano performance. *Journal of Research in Music Education, 38*(3), 187-196.

Cohen, D. A., Pascual-Leone, A., Press, D. Z., & Robertson, E. M. (2005). Off-line learning of motor-skill memory: A double dissociation of goal and movement. *Proceedings of the National Academy of Sciences, 102*(50), 18237-18241.

Davis, C. M. (2007). *Five-minute rest intervals enhance performance of brief keyboard sequences*. Unpublished Dissertation, The University of Texas at Austin, Austin.

Donchin, O., Sawaki, L., Madupu, G., Cohen, L. G., & Shadmehr, R. (2002). Mechanisms influencing acquisition and recall of motor memories. *Journal of Neurophysiology, 88*(4), 2114-2123.

Dorfberger, S., Adi-Japha, E., & Karni, A. (2007). Reduced susceptibility to interference in the consolidation of motor memory before adolescence. *PloS ONE, 2*(2), e240.

Doyon, J., & Benali, H. (2005). Reorganization and plasticity in the adult brain during learning of motor skills. *Current Opinion in Neurobiology, 15*(2), 161.

Doyon, J., Song, A. W., Karni, A., Lalonde, F., Adams, M. M., & Ungerleider, L. G. (2002). Experience-dependent changes in cerebellar contributions to motor sequence learning. *Proceedings of the National Academy of Sciences, 99*(2), 1017-1022.

Doyon, J., Ungerleider, L. G., Squire, L. R., & Schacter, D. L. (2002). Functional anatomy of motor skill learning. In *Neuropsychology of memory (3rd ed.)*. (pp. 225): Guilford Press.

Duke, R., & Davis, C. (2006). Procedural memory consolidation in the performance of brief keyboard sequences. *Journal of Research in Music Education, 54*(2), 111-124.

Duke, R., Davis, C., & Simmons, A. (2005). *Musicians' Practice Strategies and Retention of Motor Skills*. Paper presented at the Music Teachers National Association Convention.

Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B., & Taub, E. (1995). Increased cortical representation of the fingers of the left hand in string players. *Science, 270*(5234), 305.

Ellenbogen, J. M., Payne, J. D., & Stickgold, R. (2006). The role of sleep in declarative memory consolidation: passive, permissive, active or none? *Current Opinion in Neurobiology, 16*(6), 716-722.

Ericsson, K. A., & Charness, N. (1994). Expert performance: Its structure and acquisition. *American Psychologist, 49*(8), 725-747.

Ericsson, K. A., Krampe, R. T., & Tesch-Romer, C. (1993). The role of deliberate practice in the acquisition of expert performance. *Psychological Review, 100*(3), 363-406.

Fischer, S., Hallschmid, M., Elsner, A. L., & Born, J. (2002). Sleep forms memory for finger skills. *Proceedings of the National Academy of Sciences, 99(18)*.

Fischer, S., Nitschke, M. F., Melchert, U. H., Erdmann, C., & Born, J. (2005). Motor memory consolidation in sleep shapes more effective neuronal representations. *Journal of Neuroscience, 25*(49), 11248-11255.

Floyer-Lea, A., Wylezinska, M., Kincses, T., & Matthews, P. M. (2006). Rapid modulation of GABA concentration in human sensorimotor cortex during motor learning. *Journal of Neurophysiology, 95*, 1639-1644.

Fogel, S. M., Jacob, J., & Smith, C. T. (2001). Increased sleep spindle activity following simple motor procedural learning in humans. *Proceedings of the Congress Physiological Basis for Sleep Medicine, 7*, 123.

Fogel, S. M., & Smith, C. T. (2006). Learning-dependent changes in sleep spindles and Stage 2 sleep. *Journal of Sleep Research, 15*(3), 250-255.

Fonseca, R., Nägerl, U. V., Morris, R. G. M., & Bonhoeffer, T. (2004). Competing for Memory Hippocampal LTP under Regimes of Reduced Protein Synthesis. *Neuron, 44*(6), 1011-1020.

Gais, S., Plihal, W., Wagner, U., & Born, J. (2000). Early sleep triggers memory for early visual discrimination skills. *Nature Neuroscience, 3*, 1335-1339.

Giuffrida, C. G., Shea, J. B., & Fairbrother, J. T. (2002). Differential transfer benefits of increased practice for constant, blocked, and serial practice schedules. *Journal of Motor Behavior, 34*(4), 353-365.

Goins, K. R. (2006). *Familiarity with a melody prior to training increases children's piano performance accuracy*. Unpublished Dissertation, The University of Texas at Austin, Austin.

Grafton, S. T., Mazziotta, J. C., Presty, S., Friston, K. J., Frackowiak, R. S., & Phelps, M. E. (1992). Functional anatomy of human procedural learning determined with regional cerebral blood flow and PET. *Journal of Neuroscience, 12*(7), 2542-2548.

Graybiel, A. M. (1995). Building action repertoires: memory and learning functions of the basal ganglia. *Current Opinion in Neurobiology, 5*(6), 733-741.

Hauptmann, B., & Karni, A. (2002). From primed to learn: The saturation of repetition priming and the induction of long-term memory. *Cognitive Brain Research, 13*(3), 313-322.

Hauptmann, B., Reinhart, E., Brandt, S. A., & Karni, A. (2005). The predictive value of the leveling off of within-session performance for procedural memory consolidation. *Cognitive Brain Research, 24*(2), 181-189.

Hewitt, M. P. (2001). The effects of modeling, self-evaluation, and self-listening on junior high instrumentalists' music performance and practice attitude. *Journal of Research in Music Education, 49*(4), 307-322.

Hoddes, E., Zarcone, V., Smythe, H., Phillips, R., & Dement, W. C. (1973). Quantification of sleepiness: a new approach. *Psychophysiology, 10*(4), 431-436.

Hotermans, C., Peigneux, P., Maertens de Noordhout, A., Moonen, G., & Maquet, P. (2006). Early boost and slow consolidation in motor skill learning. *Learning & Memory, 13*(5), 580.

Hund-Georgiadis, M., & Yves von Cramon, D. (1999). Motor-learning-related changes in piano players and non-musicians revealed by functional magnetic-resonance signals. *Experimental Brain Research, 125*(4), 417-425.

Jerusalinsky, D., Quillfeldt, J. A., Walz, R., Da Silva, R. C., Medina, J. H., & Izquierdo, I. (1994). Post-training intrahippocampal infusion of protein kinase C inhibitors causes amnesia in rats. *Behavioral and Neural Biology, 61*(2), 107-109.

Karni, A., Meyer, G., Jezzard, P., & Adams, M. M. (1995). Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature, 377*(6545), 155-158.

Karni, A., Meyer, G., Rey-Hipolito, C., Jezzard, P., Adams, M. M., Turner, R., et al. (1998). The acquisition of skilled motor performance: Fast and slow experience-driven changes in primary motor cortex. *Proceedings of the National Academy of Sciences, 95*, 861-868.

Karni, A., Tanne, D., Rubenstien, B. S., & Askenasy, J. J. M. (1994). Dependence on REM sleep of overnight improvement of a perceptual skill. *Science, 265*(5172), 679-682.

Kelly, A. M. C., & Garavan, H. (2005). Human functional neuroimaging of brain changes associated with practice. *Cerebral Cortex, 15*(8), 1089-1102.

Kerr, R., & Booth, B. (1978). Specific and varied practice of motor skill. *Perceptual & Motor Skills, 46*(2), 395-401.

Korman, M., Raz, N., Flash, T., & Karni, A. (2003). Mutliple shifts in the representation of a motor sequence during the acquisition of skilled performance. *Proceedings of the National Academy of Sciences, 100*(21), 12492–12497.

Kuriyama, K., Stickgold, R., & Walker, M. P. (2004). Sleep-dependent learning and motor-skill complexity. *Learning & Memory, 11*(6), 705-713.

Lai, Q., & Shea, C. H. (1998). Generalized motor program (GMP) learning: Effects of reduced frequency of knowledge of results and practice variability. *Journal of Motor Behavior, 30*(1), 51-59.

Lehericy, S., Benali, H., Van de Moortele, P. F., Pelegrini-Issac, M., Waechter, T., Ugurbil, K., et al. (2005). Distinct basal ganglia territories are engaged in early and advanced motor sequence learning. *Proceedings of the National Academy of Sciences, 102*(35), 12566-12571.

Madsen, C. K. (2004). A 30-year follow-up study of actual applied music practice versus estimated practice. *Journal of Research in Music Education, 52*(1), 77-88.

Maquet, P., Laureys, S., Peigneux, P., Fuchs, S., Petiau, C., Phillips, C., et al. (2000). Experience-dependent changes in cerebral activation during human REM sleep. *Nature Neuroscience, 3*(8), 831-836.

Max/MSP. (2007). Retrieved April 3, 2007, from http://www.cycling74.com/downloads/maxmsp.

Maynard, L. M. (1999). Methods of practice used by high school, college, and professional level string players. *Texas Music Education Research*, 57-63.

McGaugh, J. L. (2000). Memory--a century of consolidation. *Science, 287*(5451), 248-251.

McNevin, N. H., Shea, C. H., & Wulf, G. (2003). Increasing the distance of an external focus of attention enhances learning. *Psychological Research, 67*(1), 22-29.

McPherson, G. E. (2005). From child to musician: skill development during the beginning stages of learning an instrument. *Psychology of Music, 33*(1), 5.

Mednick, S., Nakayama, K., & Stickgold, R. (2003). Sleep-dependent learning: A nap is as good as a night. *Nature Neuroscience, 6*(7), 697-698.

Meeter, M., & Murre, J. (2004). Consolidation of long-term memory: evidence and alternatives. *Psychological Bulletin, 130*(6), 843-857.

Miall, R. C., Jenkinson, N., & Kulkarni, K. (2004). Adaptation to rotated visual feedback: a re-examination of motor interference. *Experimental Brain Research, 154*(2), 201-210.

Miklaszewski, K. (1989). A case study of a pianist preparing a musical performance. *Psychology of Music, 17*(2), 95.

Milekic, M., & Alberini, C. (2002). Temporally graded requirement for protein synthesis following memory reactivation. *Neuron, 36*, 521-525.

Misanin, J. R., Miller, R. R., & Lewis, D. J. (1968). Retrograde amnesia produced by electroconvulsive shock after reactivation of a consolidated memory trace. *Science, 160*(3827), 554.

Muellbacher, W., Ziemann, U., Wissel, J., Dang, N., Kofler, M., Facchini, S., et al. (2002). Early consolidation in human primary motor cortex. *Nature, 415*(6872), 640-644.

Mueller, R.-A., Kleinhaus, N., Pierce, K., Kemmotsu, N., & Courchesne, E. (2002). Functional MRI of motor sequence acquisition: Effects of learning stage and performance. *Cognitive Brain Research, 14*(2), 277-293.

Pantev, C., Engelien, A., Candia, V., & Elbert, T. (2001). Representational cortex in musicians: Plastic alterations in response to musical practice. *Annals of the New York Academy of Sciences, 930*(1), 300-314.

Parsons, L. M. (2001). Exploring the functional neuroanatomy of music performance, perception, and comprehension. *Annals of the New York Academy of Sciences, 930*(1), 211-231.

Pascual-Leone, A., Dang, N., Cohen, D. A., Brasil-Neto, A., & Hallett, M. (1995). Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquistion of new fine motor skills. *Journal of Neurophysiology, 74*(3), 1037-1045.

Peigneux, P., Laureys, S., Fuchs, S., Destrebecqz, A., Collette, F., Delbreuck, X., et al. (2003). Learned material content and acquisition level modulate cerebral reactivation during posttraining rapid-eye-movements sleep. *NeuroImage, 20*, 125-134.

Peigneux, P., Orban, P., Balteau, E., Degueldre, C., Luxen, A., Laureys, S., et al. (2006). Offline persistence of memory-related cerebral actvity during active wakefulness. *PLoS Biology, 4*(4), 0647-0658.

Penhune, V. B., & Doyon, J. (2002). Dynamic cortical and subcortical networks in learning and delayed recall of timed motor sequences. *Journal of Neuroscience, 22*(4), 1397-1406.

Petersen, S. E., Van Mier, H., Fiez, J. A., & Raichle, M. E. (1998). The effects of practice on the functional anatomy of task performance. *Proceedings of the National Academy of Sciences, 95*, 853-860.

Przybyslawski, J., Roullet, P., & Sara, S. (1999). Attenuation of emotional and nonemotional memories after their reactivation: Role of beta adrenergic receptors. *Journal of Neuroscience, 19*(15), 6623-6628.

Puckette, M., & Zicarelli, D. (2004). Max/MSP (Version 4.6.3). San Francisco, CA: Cycling '74/IRCAM.

Puttemans, V., Wenderoth, N., & Swinnen, S. P. (2005). Changes in brain activation during the acquisition of a multifrequency bimanual coordination task: From the

cognitive stage to advanced levels of automaticity. *Journal of Neuroscience, 25*(17), 4270-4278.

Riccio, D. C., Millin, P. M., & Gisquet-Verrier, P. (2003). Retrograde amnesia: forgetting back. *Current Directions in Psychological Science, 12*(2), 41-44.

Robertson, E. M., Pascual-Leone, A., & Press, D. Z. (2004). Awareness modifies the skill-learning benefits of sleep. *Current Biology, 14*, 208-212.

Robertson, E. M., Press, D. Z., & Pascual-Leone, A. (2005). Off-line learning and the primary motor cortex. *Journal of Neuroscience, 25*(27), 6372-6378.

Rodriguez-Ortiz, C., De la Cruz, V., Gutierrez, R., & Bermudez-Rattoni, F. (2005). Protein synthesis underlies post-retrieval memory consolidation to a restricted degree only when updated information is obtained. *Learning & Memory, 12*, 533-537.

Rosenthal, R. K. (1984). The relative effects of guided model, model only, guide only, and practice only treatments on the accuracy of advanced instrumentalists' musical performance. *Journal of Research in Music Education, 32*(4), 265-273.

Rosenthal, R. K., Wilson, M., Evans, M., & Greenwalt, L. (1988). Effects of different practice conditions on advanced instrumentalists' performance accuracy. *Journal of Research in Music Education, 36*(4), 250-257.

Ross, S. L. (1985). The effectiveness of mental practice in improving the performance of college trombonists. *Journal of Research in Music Education, 33*(4), 221-230.

Rubin-Rabson, G. (1939). Studies in the psychology of memorising piano music: I. A comparison of the unilateral and co-ordinated approach. *Journal of Educational Psychology, 30*(5).

Rubin-Rabson, G. (1940). Studies in the psychology of memorizing piano music: A comparison of massed and distributed practice. *Journal of Educational Psychology, 31*(4), 270-284.

Rubin-Rabson, G. (1941a). Studies in the psychology of memorising piano music: IV. The effect of incentive. *Journal of Educational Psychology*.

Rubin-Rabson, G. (1941b). Studies in the psychology of memorizing piano music: A comparison of pre-study periods of varied length. *Journal of Educational Psychology, 32*, 593-602.

Rubin-Rabson, G. (1941c). Studies in the psychology of memorizing piano music: A comparison of three degrees of overlearning. *Journal of Educational Psychology, 32*, 688-696.

Sara, S. (2000). Retrieval and reconsolidation: Toward a neurobiology of remembering. *Learning & Memory, 7*, 73-84.

Savion-Lemieux, T., & Penhune, V. B. (2005). The effects of practice and delay on motor skill learning and retention. *Experimental Brain Research, 161*, 423-431.

Schlaug, G. (2001). The brain of musicians: A model for functional and structural adaptation. *Annals of the New York Academy of Sciences, 930*(1), 281-299.

Shadmehr, R., & Brashers-Krug, T. (1997). Functional stages in the formation of human long-term motor memory. *Journal of Neuroscience, 17*(1), 409.

Shadmehr, R., & Holcomb, H. H. (1997). Neural correlates of motor memory consolidation. *Science, 277*(5327), 821-825.

Shea, C. H., Kohl, R., & Indermill, C. (1990). Contextual interference: Contributions of practice. *Acta Psychologica, 73*(2), 145-157.

Shea, C. H., & Wulf, G. (1999). Enhancing motor learning through external-focus instructions and feedback. *Human Movement Science, 18*(4), 553-571.

Shea, J. B., & Graf, R. C. (1994). A model for contextual interference effects in motor learning. In *Reynolds, Cecil R (Ed) (1994) Cognitive assessment: A multidisciplinary perspective Perspectives on individual differences (pp 73-87).*

Siegel, J. (2005). Clues to the functions of mammalian sleep. *Nature, 437*, 1264-1271.

Simmons, A. (2007). *Effects of practice variability and distribution of practice on musicians' performance of a procedural skill*. Unpublished dissertation, The University of Texas at Austin, Austin.

Simmons, A., & Duke, R. (2006). Effects of sleep on performance of a keyboard melody. *Journal of Research in Music Education, 54*(3), 257-269.

Sloboda, J. A., Davidson, J. W., Howe, M. J. A., & Moore, D. G. (1996). The role of practice in the development of performing musicians. *British journal of psychology, 87*(2), 287-309.

Smith, C. (2005). Consolidation enhancement: Which states for which tasks? *Behavioral and Brain Sciences, 28*(1), 83-84.

Smith, C., & MacNeill, C. (1994). Impaired motor memory for a pursuit rotor task following Stage 2 sleep loss in college students. *Journal of Sleep Research, 3*(4), 206-213.

Stickgold, R., James, L., & Hobson, J. A. (2000). Visual discrimination learning requires sleep after training. *Nature Neuroscience, 3*(12), 1237-1238.

Stickgold, R., Whidbee, D., Schirmer, B., Patel, V., & Hobson, J. A. (2000). Visual discrimination task improvement: A multi-step process occurring during sleep. *Journal of Cognitive Neuroscience, 12*(2), 246-254.

Suzuki, A., Josselyn, S., Frankland, P., Masushiage, S., Silva, A., & Kida, S. (2004). Memory reconsolidation and extinction have distinct temporal and biochemical signatures. *Journal of Neuroscience, 24*(20), 4787-4795.

Swinnen, S. P., Schmidt, R. A., Nicholson, D. E., & Shapiro, D. C. (1990). Information feedback for skill acquisition: Instantaneous knowledge of results degrades learning. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 16*(4), 706-716.

Trepel, C., & Racine, R. J. (1999). Blockade and disruption of neocortical long-term potentiation following electroconvulsive shock in the adult, freely moving rat. *Cerebral Cortex, 9*(3), 300-305.

Van Mier, H., Perlmutter, J., & Petersen, S. E. (2004). Functional changes in brain activity during acquisition and practice of movement sequences. *Motor Control, 8*(4), 500-520.

Vertes, R. P., & Eastman, K. E. (2000). The case against memory consolidation in REM sleep. *Behavioral & Brain Sciences, 23*(6), 867-876.

Walker, M. P. (2005). A refined model of sleep and the time course of memory formation. *Behavioral and Brain Sciences, 28*(01), 51-64.

Walker, M. P., Brakefield, T., Hobson, J. A., & Stickgold, R. (2003). Dissociable stages of human memory consolidation and reconsolidation. *Nature, 425*(6958), 616-620.

Walker, M. P., Brakefield, T., Morgan, A., Hobson, J. A., & Stickgold, R. (2002). Practice with sleep makes perfect: Sleep-dependent motor skill learning. *Neuron, 35*, 205-211.

Walker, M. P., Brakefield, T., Seidman, J., Morgan, A., Hobson, J. A., & Stickgold, R. (2003). Sleep and the time course of motor skill learning. *Learning & Memory, 10*(4), 275-284.

Walker, M. P., & Stickgold, R. (2004). Sleep-dependent learning and memory consolidation. *Neuron, 44*(1), 121-133.

Walker, M. P., & Stickgold, R. (2006). Sleep, memory, and plasticity. *Annual Review of Psychology, 57*, 139-166.

Walker, M. P., Stickgold, R., Alsop, D., Gaab, N., & Schlaug, G. (2005). Sleep-dependent motor memory plasticity in the human brain. *Neuroscience, 133*, 911-917.

Williamon, A. (2002). Shifting the focus of attention between levels of musical structure. *European Journal of Cognitive Psychology, 14*(4), 493-520.

Williamon, A., & Valentine, E. (2000). Quantity and quality of musical practice as predictors of performance quality. *British Journal of Psychology, 91*(3), 353-376.

Wulf, G., Lee, T. D., & Schmidt, R. A. (1994). Reducing knowledge of results about relative versus absolute timing: Differential effects on learning. *Journal of Motor Behavior, 26*(4), 362-369.

Wulf, G., Mc Connel, N., Gartner, M., & Schwarz, A. (2002). Enhancing the learning of sport skills through external-focus feedback. *Journal of Motor Behavior, 34*(2), 171.

Wulf, G., & Prinz, W. (2001). Directing attention to movement effects enhances learning: A review. *Psychonomic Bulletin & Review, 8*(4), 648-660.

Young, D., Cohen, M., & Husak, W. (1993). Contextual interference and motor skill acquisition: On the processes that influence retention. *Human Movement Science, 12*(5), 577-600.

Vita

Sarah Elizabeth Allen was born in Pascagoula, Mississippi on August 3, 1977. She is the daughter of Carolyn Becker Callan and Leonard Joseph Callan, and has one brother, Andrew Joseph Callan. Growing up, Sarah had the opportunity to live in Connecticut, Arkansas, and Washington, D.C., but attended junior high and high school in Arlington, Texas. She graduated from Lamar High School in 1995, and began her undergraduate studies at The University of Texas at Austin, where she earned a Bachelor of Music degree in Music Studies in May 2000. In the following years, Sarah taught middle school band in Pflugerville, Texas at Westview Middle School. She married Brandon James Allen in June 2002, and began graduate school at The University of Texas at Austin in August 2003. She earned her Masters of Music in Music and Human Learning in December 2005. Sarah will be joining the faculty at Southern Methodist University, Dallas, Texas, in the Fall of 2007, where she will be an Assistant Professor in Music Education.

Permanent address: 6968 Bob O Link Drive, Dallas, Texas, 75214

This dissertation was typed by the author.